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University of Alaska Fairbanks, 1987

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THE EFFECT OF DIET ON ENERGY PARTITIONING IN MOOSE

A
THESIS

Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By
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Fairbanks, Alaska

May 1987

THE EFFECT OF DIET ON ENERGY PARTITIONING IN MOOSE

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ABSTRACT

Moose (Alces alces) have dynamic seasonal patterns of food intake and body weight changes. Body weight may vary by 35% from winter lows to summer highs. Food intake levels during summer may exceed winter levels by up to a factor of 5. Forage quality and availability are thought to drive the seasonal patterns of food intake and weight loss.

Changes in digestive strategy of moose in winter and spring were analyzed in this thesis. During December, the total mean retention time (TMRT) of food in the alimentary tract increased as dry matter intake decreased, while alimentary fill remained constant. In contrast, during April TMRT did not increase with increased intake; rather, alimentary fill increased. There appeared to be a seasonal digestive strategy for optimizing nutrient intake.

True basal metabolic rate (TBM) was estimated using regression analysis of heat production on metabolizable energy intake. TBM was estimated at 68.8, close to the interspecies mean of 70 (kcal/kg BW^{0.75}/d). However, differences in TBM noted during December, February, and April were not significant.

Paper birch (Betula papyrifera) twigs were collected during winter and cut from the tip to 8 specific diameters (2-9 mm), and analyzed for neutral detergent fiber, acid

detergent fiber, crude protein, acid detergent lignin, ash, and in vitro dry matter disappearance. Results indicated that dietary quality decreased with increasing diameter. Moose subjected to 4 different stocking rates (23, 31, 41, and 66% utilization of paper birch) showed no difference in the diameter of paper birch (mean = 2.66 mm) harvested.

A simulation model was presented in which food intake by moose was controlled by both physiological demands and alimentary capacity. Seasonal estimates of food intake changed with energy demands. The model proved useful in estimating seasonal energy requirements of moose.

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In Life You Have One Good Horse
One Good Dog
And If You're Lucky One Good Woman

L.N. Sikes

I am a lucky man, Amy;
thanks for the best 7 years of my life.

INTRODUCTION

Moose (Alces alces) are the largest living members of the family Cervidae and have a circumpolar distribution. In Alaska, moose are an important big game species, providing recreational opportunities and food for many Alaskans. There are approximately 60,000 moose distributed throughout the state with about 5,000 moose harvested yearly for human consumption.

In southcentral Alaska, shrub and early successional forest vegetation is the preferred moose habitat and is mainly perpetuated by fires, flooding, and avalanches (LeResche et al. 1974). In the natural sequence, new habitat remains highly productive for 25 to 35 years, and in the latter half of this period it is dominated by paper birch (Betula papyrifera) (Oldemeyer and Regelin 1986).

In Alaska, urban sprawl, geological development, and hydro-electrical development are reducing the amount of moose habitat. Fire suppression also reduces the amount of early successional plant communities that are in many instances prime moose habitat. In addition, a growing human population has increased demands for a greater moose harvest. These factors have caused moose management in Alaska to change from passive monitoring to intensive management with habitat enhancement and predator management programs.

To understand moose population dynamics and how removal of land from productive moose habitat affects populations, it is essential to know the carrying capacity of the land (i.e., maximum number of moose that can live and reproduce per unit area on a sustainable basis). Carrying capacity can be calculated by estimating the forage available and the efficiency of the animal in processing that forage, ultimately converting a percentage of it to excess animals for harvest. In the process, the ingested forage is partitioned into energy necessary for maintenance, growth, and reproduction.

Fancy (1986) conducted a sensitivity analysis on a model of caribou (Rangifer tarandus) energy budgets and found that food intake, food digestibility, and fasting metabolic rate had the greatest effects on animal production. Understanding the implications of diet digestibility, food intake, and basal metabolism for maintenance and production necessitates partitioning energy flows in the animal. Knowledge about factors controlling food intake, diet digestibility, and metabolic rate are important to develop an understanding of the strategies evolved by moose to meet their seasonal energy requirements. Partitioning the flow of energy in the animal will provide insight into how these factors function and interact to determine energy requirements and carrying capacity of the range.

Control of Food Intake

Food intake is controlled ultimately by the brain (Anand 1961). Gut fill receptors in the rumen wall appear to be the primary agents ending a feeding bout in domestic ruminants (Campling 1970). High fiber diets result in shorter feeding bouts and may limit daily forage intake. However, daily forage intake increases with increasing diet digestibility. A linear increase in forage intake up to 82% digestibility has been noted for cattle (Freer 1981). Ellis (1978) reported that the rumen volume, amount of space occupied by undigested material, and rate of chemical and physical breakdown of digestible material are the factors which determine forage intake. The actual mechanism controlling this response is conjectural; however, Van Soest (1982) suggested that the rate of outflow of undigested residue from the digestive tract is the limiting factor and therefore feces output is the controlling variable.

Intake during a feeding event is not only controlled by stretch receptors in the rumen (physical control) but also by physiological factors, again integrated by the central nervous system (Montgomery and Baumgardt 1965). The critical level where control of intake switches from physical control (i.e., gut fill) to physiological control varies with animal energy requirements (Robbins 1983).

Moose in captivity have demonstrated a seasonality of intake when offered high-quality food year-round (Schwartz et al. 1984). Peak forage intake occurs in summer and coincides with high forage availability and quality; it reaches a low point during winter (Jan-Mar), a period of low forage quality and often low availability. This seasonality in appetite is positively related with availability and quality of the forage resources, and is not only apparent in moose, but in several other wild ruminants (Wood et al. 1962, Bandy et al. 1970, McEwan and Whitehead 1970, Ozoga and Verme 1970, Westra and Hudson 1981, Wheaton and Brown 1983).

Seasonal changes in weight have been reported for moose by Franzmann et al. (1978) and Schwartz et al. (1984). It is clear that northern ruminants have evolved physiological mechanisms to store energy and protein when they are readily available to serve as a reserve during periods of nutrient shortage.

Food Quality

For herbivores, foods are not equal in their capacity to support animal functions of maintenance, growth, and reproduction. Diets supply energy and essential nutrients (i.e., nitrogen, minerals, vitamins). Of these, energy is most often the limiting factor for the herbivore.

Evaluation of forage quality by chemical analysis is most often done as described by Van Soest (1967). This method is based on the anatomy of the plant cell in relation to the nutritive availability of the different chemical components in a plant cell. The Van Soest system separates the plant into cell wall and cell contents. The cell contents consist of lipids, sugars, pectin, starch, non-protein nitrogen, and protein. The cell contents are considered to be 98-100% digestible (Van Soest 1967). The cell wall component contains hemicellulose, fiber-bound protein, cellulose, lignin, and lignified nitrogen. Cell walls are digested by microbes in the rumen; their ability to digest lignin-associated proteins and carbohydrates depends on the extent of lignification.

Plants have evolved defense mechanisms for protection against herbivory. Many plants contain substances that inhibit digestion by impeding enzymatic digestion. Lignin, cutin, suberin, and biogenic silica are plant structural components that physically inhibit digestion. Plants also contain chemicals that prevent or reduce microbial digestion. These digestive inhibitory materials are often termed secondary chemicals because they are produced as metabolic by-products of the plants. Secondary chemicals are a heterogeneous mix of small molecular weight compounds that interfere with microbial digestion, growth, and reproduction (Freeland and Janzen 1974, Scott 1974).

Plant defense mechanisms often deter herbivory, thereby influencing dietary selection (Bryant and Kuropat 1980). Foraging and dietary selection theory is based on optimization of energy cost-benefit functions (Krebs 1978). However, animal selectivity of dietary constituents may not be directly related to optimal nutrient acquisition alone, but to a complex relationship between nutrient content, forage quantity, and secondary chemical avoidance.

Metabolic Rate

Fasting metabolic rate (FMR) is the most important component of the daily energy budget of the ruminant (Blaxter 1962, Kleiber 1975). Determining the mechanism that controls FMR is necessary to gain an understanding of the seasonal dynamics of weight change and feed intake.

Using classical methods of calorimetry, Regelin et al. (1985) have shown seasonal changes in FMR with moose. These findings support previous data for roe deer (Capreolus capreolus; Weiner 1977), white-tailed deer (Odocoileus virginianus; Silver et al. 1969), and caribou (McEwan and Whitehead 1970). Regelin et al. (1985) reported FMR of moose varied by 88% from summer highs to winter lows. Though food intake was not measured in the study, peak FMR coincided with expected peak intakes measured in other studies with moose (Schwartz et al. 1984).

Seasonal fluctuations in forage quality and forage quantity coincide with seasonal FMR. Whether the 88% seasonal variation in FMR reported for moose (Regelin et al. 1985) are seasonal (i.e., photoperiod) or related to food quality or food quantity is unknown. Understanding factors that influence seasonal FMR is important for determining seasonal energy partitioning.

Hypotheses

The purpose of this study was to investigate the effect of diet quality and quantity on energy partitioning in moose. There were 3 hypotheses tested during the study:

1) Nutritive quality of available forage decreases as the level of forage utilization increases.

In Chapter 1 data are presented on the nutritive value of paper birch in relation to 4 different moose stocking rates at the Moose Research Center, Kenai Peninsula, Alaska. The influence of browsing diameter on nutritive quality of paper birch is presented.

2) As forage intake decreases, passage rate through the alimentary tract decreases, which serves to increase diet digestibility.

Chapter 2 describes the results of 3 passage rate trials in which diet quality is held constant and intake is varied. The effects of intake on liquid and particulate

passage rates are presented. Also included are estimates of alimentary tract volume in relation to food intake and season.

3) As forage availability and quality decrease, fasting metabolic rate decreases to lower animal maintenance requirements.

Chapter 3 relates the influence of metabolizable energy intake on resting metabolism. Also presented are estimates of true basal metabolism, the efficiency of retention of metabolizable energy, and methodology for comparing data on metabolic rates when different techniques were employed.

Chapter 4 describes a model simulating moose metabolism which incorporates the data from chapters 2 and 3. The model generates food intake requirements to meet target body condition values. Both physical and physiological control mechanisms are invoked depending on diet quality and physiological demands to meet target (i.e., seasonal) body condition.

CHAPTER 1

WINTER NUTRITIONAL COMPOSITION OF PAPER BIRCH

INTRODUCTION

The winter browse supply and its nutritive quality are important to moose (Alces alces) range carrying capacity (LeResche et al. 1974). In Alaska, early stages of forest succession provide an abundance of excellent moose forage (i.e., aspen (Populus tremuloides) and willow (Salix spp.)). Later, the habitat is dominated by paper birch (Betula papyrifera) and birch becomes the dominant item in the moose diet under intensive utilization, even though it is less preferred than willow or aspen. Vegetation conditions become less favorable to moose 25 to 35 years following a disturbance. The birch trees grow out of reach and little understory vegetation is utilized by moose.

Winter forage quality limits forage intake for moose (Renecker and Hudson 1985). Therefore, identifying the factors controlling forage quality is important. Of particular importance is the digestibility of the forage as well as the nondigestible fiber content of the twigs.

Nutritional content of twigs from great willow (Salix caprea), European mountain ash (Sorbus aucuparia), and silver birch (Betula pendula) decrease with increasing twig diameters (Hjeljord et al. 1982). Therefore, estimation of

the nutritional content of browse in the diet of moose requires an estimation of the browsing point diameter (i.e., the diameter at which the moose breaks off the twig). Such measurements have not been made for paper birch of the Kenai Peninsula. Presumably, moose clip twigs to a point of diminishing nutritional return when moose densities are low, but may take larger diameter twigs as the forage supply declines at high moose densities.

This study was conducted to determine the moose browsing point diameters of paper birch in enclosures stocked with moose at 4 different winter densities (moose/kg paper birch available). The nutritional quality of browse consumed under each stocking rate was determined by relating the quality of whole twigs clipped at a specified diameter. Nutritional quality was inferred from measurement of in vitro dry matter disappearance (IVDMD), crude protein (CP), and fiber components.

STUDY LOCATION AND METHODS

Location

The Moose Research Center (MRC) was established in 1967 and is located on the Kenai National Wildlife Refuge about 40 miles northeast of Soldotna, Alaska. The Alaska Department of Fish and Game constructed and maintains the research facilities under a cooperative agreement with the

U.S. Fish and Wildlife Service. Four 260 ha enclosures were completed in 1971 with subsequent additions of digestion stalls, individual feeding pens, and an open circuit respiration chamber.

The MRC is located in a mixed birch-spruce forest which was burned by wildfire in 1947. Each pen is a mosaic of burned and unburned vegetation. Topography is flat to gently rolling hills in each pen. Approximately 60 ha of 1 pen was crushed by mechanical crushers in 1976 and is currently in an earlier successional stage than the other 3 pens.

Nutritional Content by Diameter

Unbrowsed paper birch twigs were collected during April 1984 outside the experimental enclosures but close to the MRC. The twigs were collected from birch trees along 1-km linear transects. Every third tree along the transect was sampled with no more than 3 twigs collected from each tree. Twigs were cut at 8 specified diameters (2-9 mm), and the entire twig from the specified diameter to the distal end was taken for analysis. This collection system emulated the observed browsing of moose.

One hundred twigs of each diameter were collected and composited by diameter for chemical analysis. Samples were dried at 50C and ground through a 40 mesh screen in a Wiley

mill. The ground samples were stored in air tight containers prior to chemical analysis.

Chemical analyses were performed at the Animal Science Nutrition Laboratory, New Mexico State University. All data are presented on a dry matter basis, with values for ash, crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) determined according to the procedures of AOAC (1980). Values for neutral detergent solubles (NDS) and hemicellulose were calculated as described by Van Soest (1967). IVDMD was done using rumen fluid from a yearling male moose that was free-ranging on winter browse prior to collection. The moose was shot in the head and the rumen fluid was maintained in the body cavity for 2 hours during transit. After transit the rumen fluid was removed and IVDMD procedures were carried out as outlined by Pearson (1970).

Moose Browse Point Diameter

This study was part of a larger, more intense vegetation study at the MRC and is reported in detail by Regelin et al. (1986). The number of marked paper birch used to estimate browsing point diameter varied from 196 to 279 in each of the 4 enclosures. Trees were marked in August and each tree was revisited in May. Following winter browsing, all moose browse points were measured to the nearest 0.01 mm.

Pre- and postbrowsing biomass were estimated from twig diameter:weight relationships. Utilization was estimated by subtracting postbrowsing biomass (i.e., twig biomass remaining after browsing) from prebrowsing biomass and dividing the difference by prebrowsing biomass.

Moose densities in the enclosures have historically varied from 0 moose/pen to 28 moose/pen. However, in the previous 5 years moose densities varied from 0 to 8 moose/pen. During the current study, moose densities in each of the pens were manipulated to remove 35%, 100%, 50%, and 75% of the winter browse forage for each of the enclosures 1, 2, 3, and 4, respectively. The stocking rates used were estimated by using predictions of forage intake based on output from a nutrient carrying capacity model proposed by Swift (1983).

Relationship of nutritional content with diameter were analyzed by the testing of 4 different regression models (Statgraphics 1985) for best fit (simple linear, multiplicative, logarithmic, and exponential models).

RESULTS AND DISCUSSION

Moose Browse Point Diameter

Moose browsing point diameter was not significantly different among the 4 different stocking rates (Table 1). The pooled mean browsing point diameter is 2.6 mm and the

Table 1. Winter stocking rates of moose (kg of forage available per moose day) and moose browse point diameter of paper birch removed by moose under 4 different stocking rates, Moose Research Center, Kenai Peninsula, Alaska, during winter 1983-84.

Pen	Stocking rate	N	Diam ^a	SD
1	7.75	194	2.64	1.180
2	2.75	195	2.55	1.100
3	5.40	100	2.50	0.945
4	5.40	82	2.83	0.958

^a Browse point diameter in mm

distribution was bell shaped, but slightly skewed right (Fig. 1). Desired utilization levels were not achieved during the study, but rather ranged from 23 to 66% utilization (Table 2; Regelin et al. 1986). These results indicate that increasing the utilization level from 23 to 66% did not increase the diameter of paper birch twigs browsed by moose but rather increased the utilization of each marked tree (Table 2).

Nutritional Content by Diameter

Nutritive analysis of paper birch showed CP and ash content declined with increasing diameter, whereas NDF and ADF content increased with increasing diameters (Table 3). The relationships between diameters and individual nutrients were tested using 4 regression models as previously described. The multiplicative model $Y = aX^b$ where Y =nutritional content, a and b are constants and X =(browse point diameter) accounted for the most variance and also had the greatest biological basis. The equations used for prediction of twig weight from a known diameter were derived from sampling paper birch twigs ($n=1600$) and were also multiplicative (Regelin et al. 1986).

A significant ($p < 0.05$) relationship was found for twig diameter with all nutritive components except ADL (Table 4). Fig. 2 shows the chemical analysis of nutritional content by

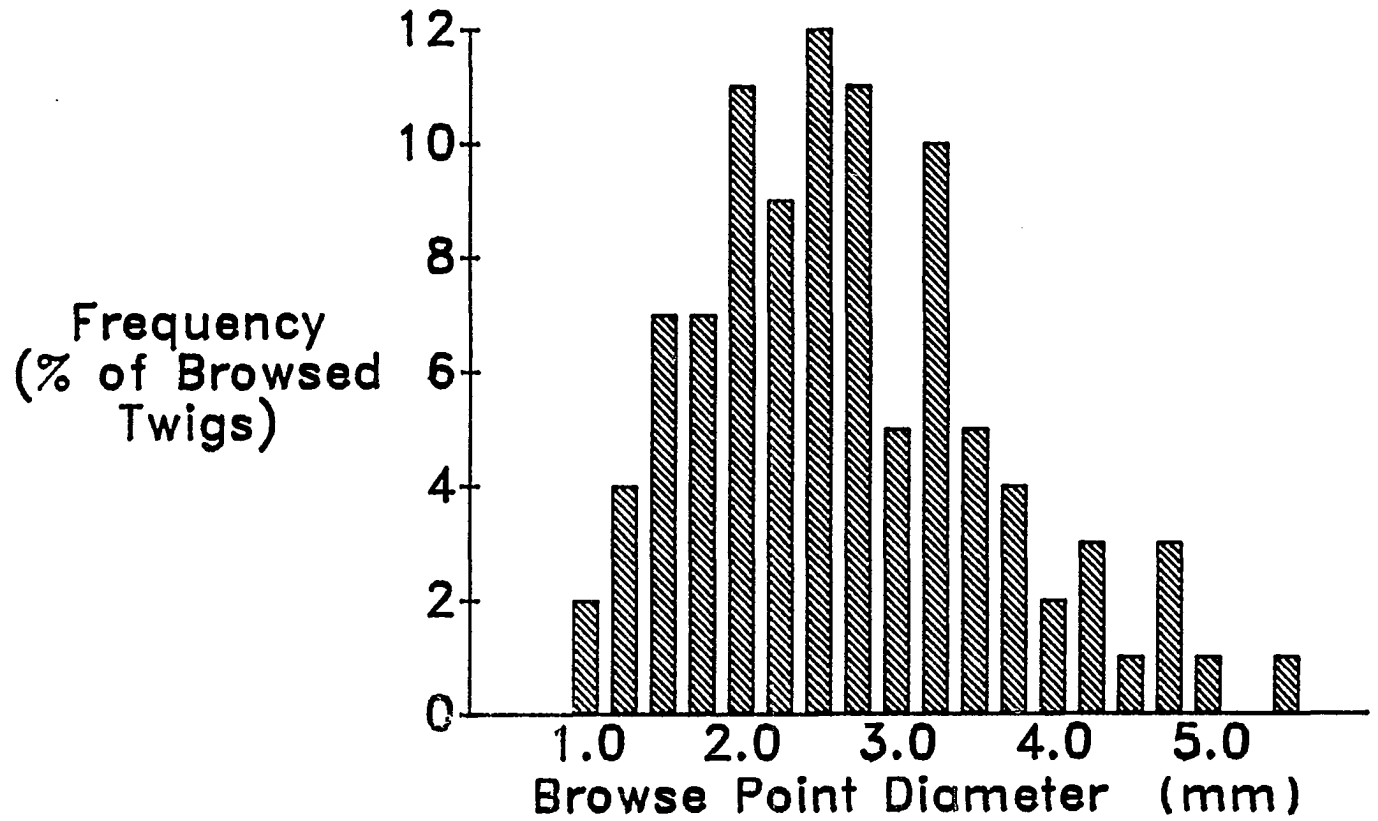


Fig. 1. Paper birch browse point diameters by moose under 4 different stocking rates, Moose Research Center, Kenai Peninsula, Alaska, winter 1984-85. (n-571)

Table 2. Comparison of 3 methods of measuring browse utilization levels of paper birch current annual growth (CAG) by moose at the Moose Research Center, Kenai Peninsula, Alaska, winter 1983-84.^a

Pen	Biomass ^b removed	Number of CAG stems browsed	Number of birch shrubs browsed
1	41 + 11	37 + 7	52 + 7
2	23 + 10	20 + 4	40 + 6
3	31 + 14	32 + 6	63 + 5
4	66 + 10	60 + 7	69 + 5

^a Regelin et al. 1986

^b Utilization + 80% confidence interval

Table 3. Nutritional content^a (dry matter basis) of twigs composited by diameter (DIAM; mm). Twigs were collected in April 1984 on the Kenai Peninsula of Alaska.

DIAM	NDS	CP	NDF	ADF	ADL	ASH	IVDMD	PDMD
2	38.2	8.3	61.8	49.3	27.7	1.96	----	37.4
3	30.4	7.5	69.6	56.2	28.7	1.54	18.9	33.4
4	29.0	6.0	71.0	56.7	29.0	1.51	19.4	32.0
5	26.3	5.9	73.7	58.7	29.5	1.38	16.7	30.0
6	22.6	5.5	77.4	61.0	25.5	1.40	16.9	34.4
7	22.5	5.5	77.5	61.3	27.2	1.36	13.8	31.5
8	20.6	4.9	79.4	64.0	28.5	1.22	14.5	29.3
9	20.3	5.1	79.7	63.6	26.1	1.26	12.6	32.7

^a NDS = Neutral detergent solubles; CP = Crude protein (% nitrogen * 6.25); NDF = Neutral detergent fiber; ADF = Acid detergent fiber; ADL = Acid detergent lignin; IVDMD = % In Vitro Dry Matter Disappearance; PDMD = Predicted apparent digestibility.

Table 4. Regression of nutritional composition of paper birch twigs (Y) on browse point diameters (X). Twigs were collected in April 1984 on the Kenai Peninsula of Alaska.

Regression model		$Y=aX^b$			
Nutritional Component ^a	n	a	b	r ²	Sig.
CP	8	10.5	-0.348	0.943	p<0.005
NDS	8	50.5	-0.422	0.999	p<0.005
NDF	8	56.6	0.164	0.960	p<0.005
ADF	8	45.4	0.160	0.943	p<0.005
ADL	8	29.4	-0.037	0.135	ns
ASH	8	2.2	-0.273	0.906	p<0.005
IVDMD	7	31.0	-0.384	0.846	p<0.005
PDMD	8	38.1	-0.099	0.434	ns

^a CP = Crude protein (% nitrogen * 6.25); NDS = Neutral detergent solubles; NDF = Neutral detergent fiber; ADF = Acid detergent fiber; ADL = Acid detergent lignin; IVDMD = In Vitro Dry Matter Disappearance; PDMD = Predicted apparent digestibility

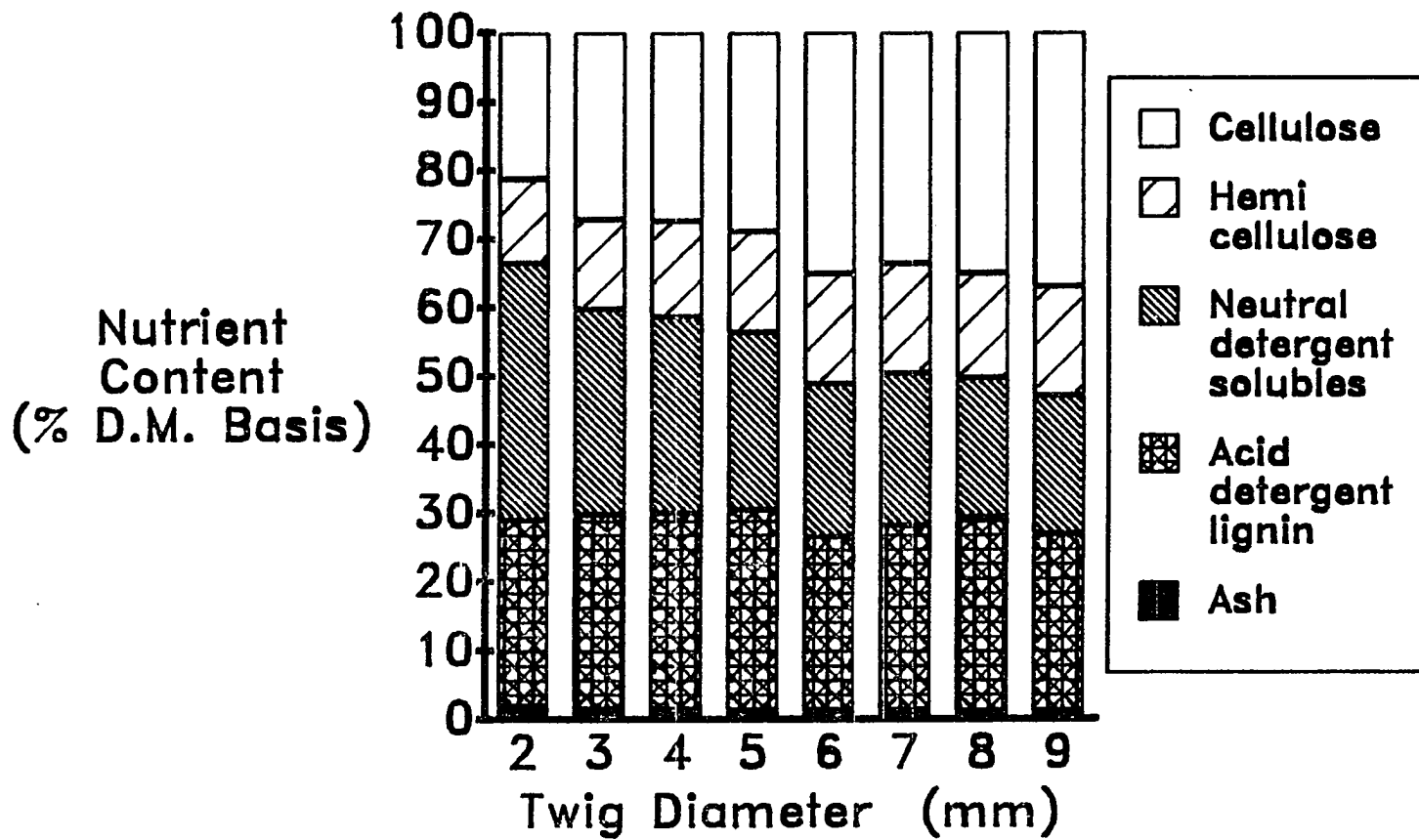


Fig. 2. Nutrient content of paper birch. One hundred samples of each diameter were composited for analysis. Twigs were collected during April 1985 on the Kenai Peninsula, Alaska.

diameter of paper birch during winter. Independent of twig diameter, ADL remained high and constant at 30%. The major constituent changes were a loss of NDS and a comparative increase in cellulose as diameter increased. This increase in less digestible material was accompanied by a decrease in IVDM with increasing twig diameter (Fig. 3).

The classical method of reporting nutritional content of browse was by nutritional analysis of current annual growth. However, the results presented here are made without consideration of current annual growth but with regard to diameter only.

Hjeljord et al. (1982) reported nutritional content by diameter of great willow, European mountain ash, and silver birch. Reanalysis of his data using a multiplicative model produced results similar to those measured in this study (Table 5). The intercepts of great willow and European mountain ash are much higher than paper birch (66.9 and 57.9 vs. 31.0%) indicating higher digestibility, whereas silver birch and paper birch were similar (32.2 vs. 31.0%). Of further interest is the greater decrease in digestibility with increasing diameter of silver birch. Great willow and European mountain ash depict a more gradual decrease in digestibility with an increasing diameter than that of paper birch or silver birch.

The IVDM of twigs with a diameter of 2.68 mm were estimated for paper birch, silver birch, great willow, and

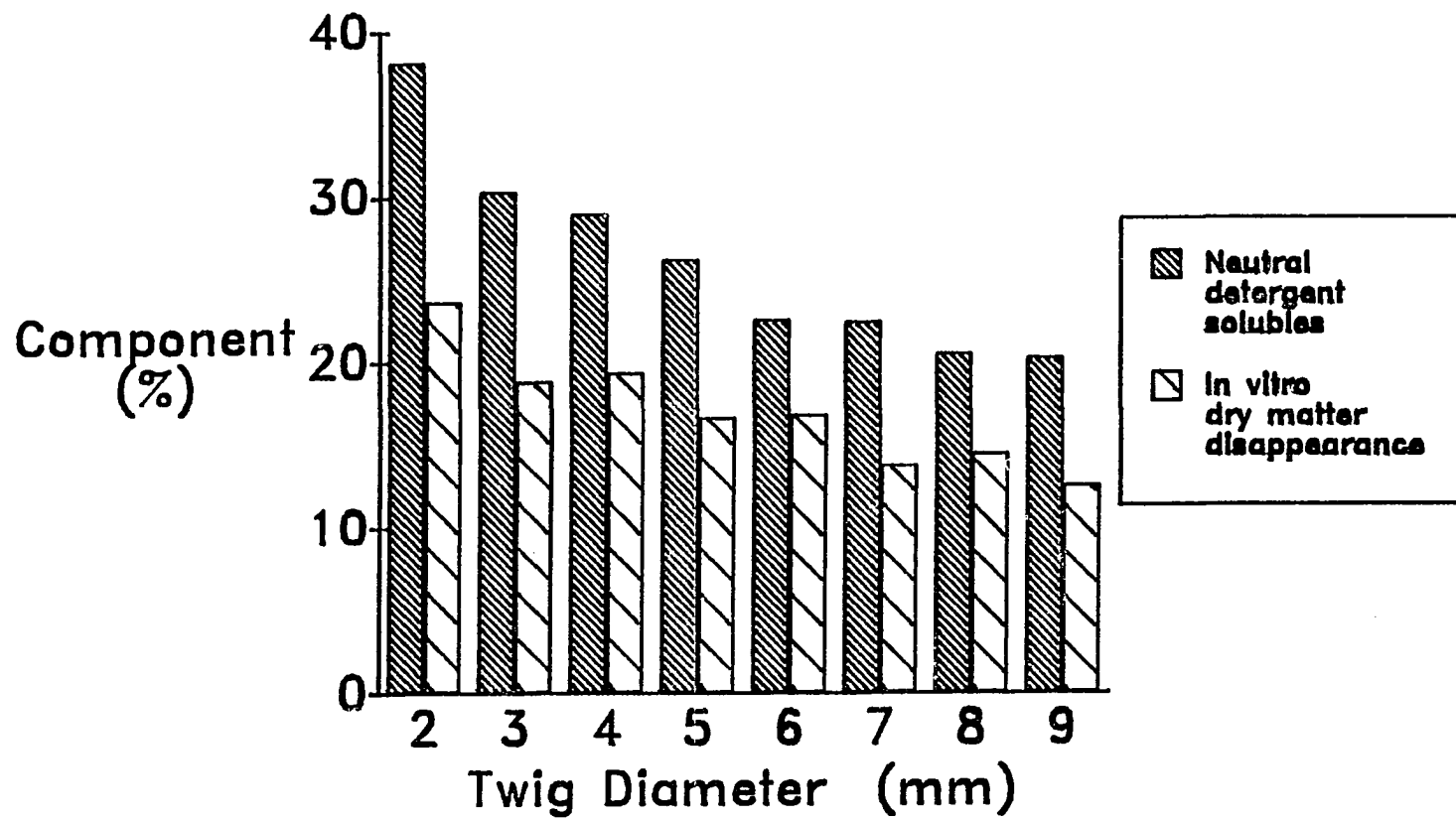


Fig. 3. Percentage nutrient detergent solubles and *in vitro* dry matter disappearance of paper birch on a dry matter basis. One hundred samples of each diameter were composited for analysis. Twigs were collected during April 1985 on the Kenai Peninsula, Alaska.

Table 5. Between-species comparison of winter In vitro dry matter disappearance (IVDMD) (Y) in relation to twig diameter (X) of paper birch, great willow, European mountain ash, and silver birch. A twig diameter of 2.68 mm (X) was used for comparison of the 4 different species.

Regression model		$Y=aX^b$				
Species	N	a	b	r^2	Sig.	IVDMD
Paper Birch	7	30.98	-0.384	0.846	$p < 0.005$	21.2
Great Willow	6	66.93	-0.338	0.922	$p < 0.005$	48.0
E. Mountain Ash	6	57.87	-0.335	0.926	$p < 0.005$	41.6
Silver Birch	6	32.23	-0.520	0.935	$p < 0.005$	19.3

European mountain ash using regression analysis techniques (Table 5). The slopes reflect changes in composition and suggest that changes are most dramatic for silver birch. The basis for differences between the birches is not known; however, a small change in the maximum point of browsing by moose results in a larger change in IVDMD for silver birch.

Nutrient content of the paper birch harvested in each of the enclosures was estimated using the mean browse point and the nutritive content equations. This estimate indicates little difference between IVDMD and CP removed from the 4 treatments (Table 6).

Digestive Inhibitors

The Van Soest fiber analysis system was developed for use with grasses and legumes (Van Soest 1967). In many instances, the chemical composition of the grasses and legumes differs considerably from woody browse (i.e., paper birch) and consequently may lead to erroneous results (Schwartz and Hobbs 1985). Robbins (1983) reported that the secondary plant chemicals are extracted with the NDS solution. This would increase the NDS fraction and overestimate the forage nutritional quality.

Paper birch is defended against herbivory by structural and secondary chemical defenses. Robbins (1983) states that

Table 6. Predicted crude protein (CP) and In Vitro Dry Matter Disappearance (IVDMD) of paper birch removed by moose under 4 different utilization levels at the Moose Research Center, Kenai Peninsula, Alaska, winter 1983-84.

Utilization (%) + 80% CI	Mean Browse Diameter (mm) (SD)	CP ^a (%)	IVDMD ^b (%)
23 + 10	2.55 (1.100)	7.6	21.6
31 + 14	2.50 (0.945)	7.6	21.8
41 + 11	2.64 (1.180)	7.5	21.3
66 + 10	2.83 (0.958)	7.3	20.9

^a Crude protein = $10.5 * (\text{browse point diameter})^{-0.348}$

^b % In vitro dry matter disappearance = $31.0 * (\text{browse point diameter})^{-0.384}$

secondary plant chemicals will reduce the apparent digestibility of NDS. Furthermore, Rhoades (1979) reported lignification will reduce digestibility of carbohydrate by impeding enzymatic digestion.

In this study, IVDMD decreased with increasing twig diameters (Fig. 2). This coincided with decreasing NDS as diameters increased (Fig. 3). NDS of grasses and legumes are 98-100% digestible in herbivores (Van Soest 1967). This suggests interference of a digestive inhibitor on digestibility of cell contents in the closed incubation in vitro system.

The possible influence of plant defense mechanisms on estimated nutritive quality is evident in the relationship of NDS to IVDMD (Fig. 4). If all fractions other than NDS are considered nondigestible, then NDS digestibility of paper birch twigs in this study was no higher than 61 to 75%. This is further substantiated by using Van Soest's (1982) calculation of apparent digestibility from chemical analysis which provides estimates 30 to 60% higher than the observed IVDMD (Table 3). This observation is in agreement with our reduced digestibility of NDS. The difference between IVDMD and digestibility calculated from fiber components suggests plant secondary compounds are reducing digestibility. However, it is possible that the Van Soest fiber analysis is not valid for shrubs and that formulas to

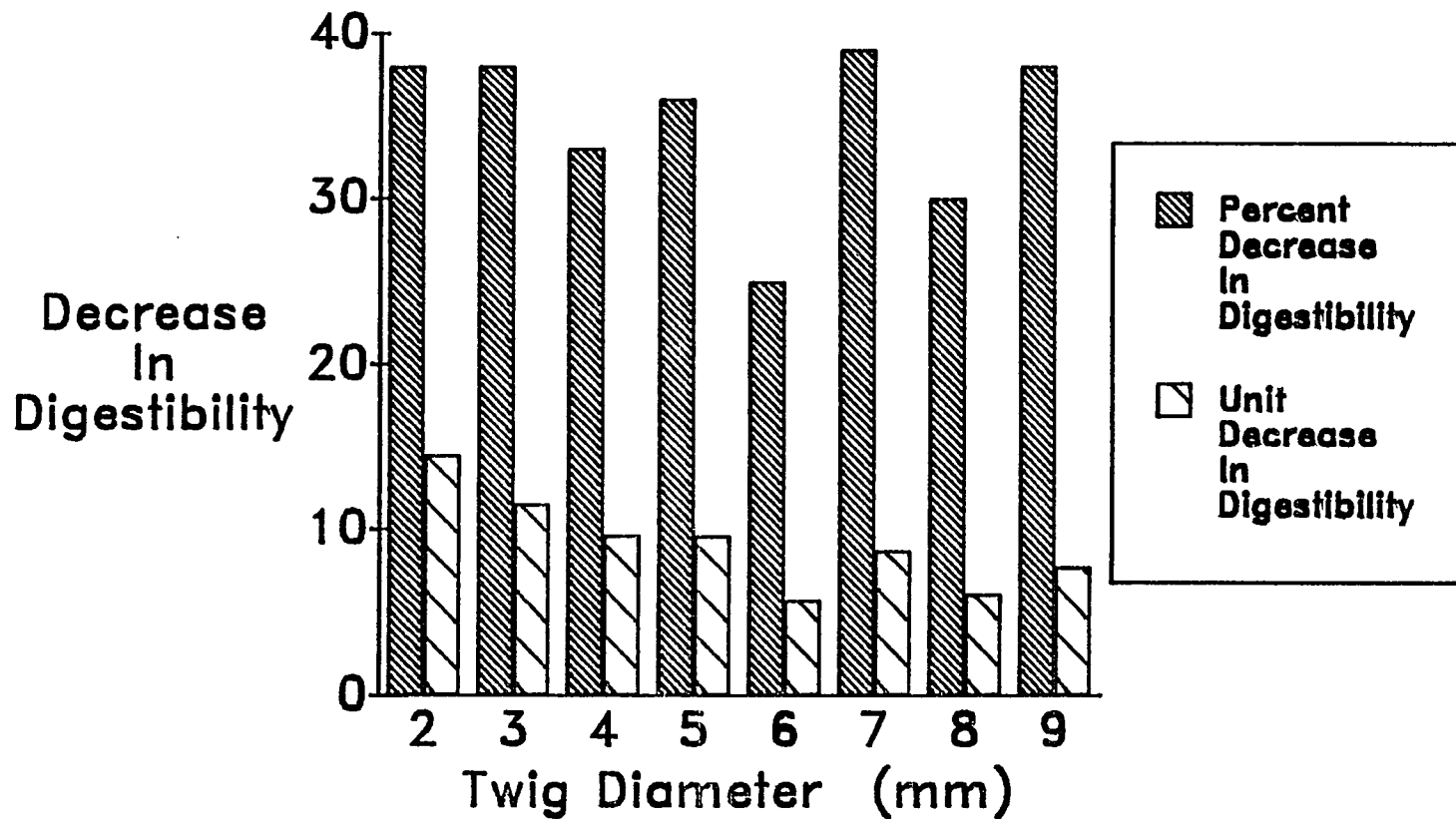


Fig. 4. Percentage and unit decrease in digestibility of paper birch by diameter. Decrease in digestibility is the difference between neutral detergent solubles and *in vitro* dry matter disappearance. One hundred samples of each diameter were composited for analysis. Twigs were collected during April 1985 on the Kenai Peninsula, Alaska.

predict digestibility from the fiber analysis are also erroneous.

Twig diameter had no significant effect on digestibility of NDS. However, if the difference between NDS and IVDMD is examined as a direct reduction rather than a percentage reduction there is a strong positive correlation between digestibility inhibitors and twig diameter (Fig. 4).

Whether NDS is overestimated in this study due to secondary compounds, or IVDMD is reduced by secondary compounds, cannot be determined. However, it is evident that secondary chemicals interfere with understanding the relationships between Van Soest fiber analysis and IVDMD.

CONCLUSIONS

Increasing utilization of paper birch from 23 to 66% did not significantly increase moose browse point diameter or decrease nutritive quality of paper birch in the diet. However, whether moose eat thicker twigs beyond 66% utilization cannot be predicted without further study.

Nutritional quality of paper birch in winter decreases with increasing diameter of the twig utilized. Therefore, people collecting browse samples for nutrition studies should report clipping diameter along with forage evaluation estimates.

Indirect evidence suggests that the most digestible dietary component (NDS) was not completely digested and it

is hypothesized that inhibitory agents were responsible. Whether plant inhibitory agents caused overestimation of the NDS component of the plant or actually reduced the digestibility of NDS is not known. However, the digestive inhibitors had a marked effect on the apparent digestibility of paper birch. The use of IVDMD in relation to potential DMD based on chemical analysis (Van Soest 1982) is a useful means to evaluate the presence and relative level of digestive inhibitors.

CHAPTER 2

EFFECT OF INTAKE ON DIGESTA RETENTION TIME IN MOOSE

INTRODUCTION

Food intake and digestibility are critical components that control the availability of energy for ruminants (Blaxter 1962, White 1983, Fancy 1986). Both the intake and digestibility of low-quality foods may be controlled by retention time in the rumen (Thornton and Minson 1972, Mertens and Ely 1978, Bull et al. 1979, Holleman et al. 1983, Grovum 1984).

In domestic livestock, rumen retention time of both the liquid and particulate phases of the digesta have been correlated with volatile fatty acid proportions and production rates (Hodgson and Thomas 1975, Isaacson et al. 1975), microbial protein synthesis (Hespell 1979), and amounts of microbial biomass flowing to the lower tract (Harrison et al. 1976, Kellaway et al. 1978). These factors are believed to control the efficiency of food energy utilization, in both the digestive and postabsorptive phases (Balch and Campling 1962, McClymont 1967, Jones 1972, Baile and Forbes 1974).

The retention time of the particulate phase affects the digestibility of the food components (Blaxter et al. 1956, Faichney and Gherardi 1986), whereas the liquid phase has

been correlated with rumen bacterial metabolic efficiency and microbial protein available to the host animal. Therefore, the determination of retention time of both the liquid and particulate digesta in the rumen and alimentary tract will provide insight into both digestion and metabolic efficiency processes.

Ruminal and alimentary fill may vary seasonally (Grovm and Williams 1973, Milne et al. 1978, Forbes et al. 1981) and with dietary specialization (Kay et al. 1979; Hoffmann 1982, 1983). These variations in rumen fill have implications for physical control over food intake through activation of stretch receptors (Campling 1970).

A new technique to estimate the amount of alimentary fill in vivo with intact animals has been developed (Holleman and White 1986) that will provide new insights into the regulation of food intake. The technique involves the use of a nondigestible particulate marker, so that digesta retention time and alimentary fill can be measured simultaneously.

Only 1 study (Schwartz et al. 1986a) has been conducted in which liquid and particle flows have been measured with moose. That study and those with reindeer (Rangifer tarandus) and muskoxen (Ovibos moschatus) indicate that liquid rumen turnover time (L-RTT) and particulate rumen turnover time (P-RTT) are highly correlated and that L-RTT is 74% to 84%

of that for the particulate phase (White et al. 1984). This observation with northern wild ruminants is in marked contrast to findings for cattle and sheep in which L-RTT is much faster than P-RTT (Balch and Campling 1965, Bull et al. 1979).

All of these northern species (moose, reindeer, and muskoxen) are to varying degrees concentrate selectors, or adaptive mixed foragers, in Hoffman's scheme of herbivory (Hoffman 1982). Particulate matter may flow more rapidly in these species because they have adopted a strategy to pass undigested materials quickly through the alimentary tract. They eat forbs and browse material which contains short lignified fibers that can be fractured rapidly into smaller particles, whereas domestic species like sheep and cattle consume a diet of grass and grass-like species containing fiber components that retard passage through the digestive tract (McCollum 1983).

White et al. (1984) reported that in winter a decline in the nutritive value and digestibility of woody browse resulted in a reduced voluntary food intake of moose while mean L-RTT increased. This inverse relationship suggested that a decline in forage quality cannot be compensated for by an increase in ruminal and/or alimentary capacity. The maintenance of alimentary tract fill appears adaptive. It appears that the winter nutrient acquisition strategy is to

optimize nutrient intake by rapid passage through the digestive tract, rather than maximizing digestion of winter forages.

Ruminal and alimentary tract fill increased in summer compared to winter in free-foraging ruminants (Staaland et al. 1979). Based on these facts, I hypothesized that a seasonal shift occurs from one of fixed ruminal/alimentary fill in winter to one of alimentary plasticity in summer as the forage quality increases. This plasticity would allow increased intake while maintaining a sufficiently long total mean retention time (TMRT) in the alimentary tract to optimize digestibility.

I tested this hypothesis by varying the intake of a low quality food in winter and spring and by measuring the transit time and alimentary fill. During winter, the rumen/alimentary fill should remain constant, independent of intake, and total mean retention time (TMRT) would be inversely related to food intake. In spring, alimentary fill should vary with food intake, and TMRT would remain constant. Testing this hypothesis would aid in understanding aspects of moose foraging strategies.

The objectives of this study were to:

- a) determine the retention time of liquid and particulate phases in the rumen and alimentary tract, and

- b) determine if there is a seasonal shift in alimentary fill and retention time in moose fed a low-quality, browse-based diet.

METHODS

The experiment was carried out at the Moose Research Center (MRC), Kenai Peninsula, Alaska. Tame, hand-raised adult (2-5 years) moose were used in all trials. Trials 1 (T1) and 2 (T2) were conducted during January and April of 1984, and trial 3 (T3) was conducted in April 1985. January was considered to represent winter, while the April trials represented the start of spring on the Kenai Peninsula. During all trials animals were held individually in 3x10 m open pens with free access to trace mineralized salt and water.

Trials One and Two

Three food intake levels were fed (treatments) to 3 moose on each treatment. Treatments levels were 70% (L), 85% of ad libitum (M), and ad libitum (H) of an identical, low quality feed. Feeding level was based on g feed/kg BW^{0.75} (MI) and recalculated weekly. The diet consisted of a pelleted ration (HQ) developed for moose (Table 7) (Schwartz et al. 1985). The ration also contained 1.25% chromium sesquioxide as an indigestible marker. Feed was

Table 7. Composition of pelleted diet (D.M. basis) fed to moose in all trials during winter 1984-85, Moose Research Center, Kenai Peninsula, Alaska.

Ingredient	% of Diet
Corn	28.7
Sawdust ^a	25.9
Oats, rolled	17.2
Soybean meal	7.2
Cane molasses	5.7
Barley	5.7
Beet pulp	5.7
Vitamin premix	0.3
Chromium sesquioxide	1.3
Pelaid ^b	1.4
Mycoban ^c	Trace
Nutritional Content	
Crude Protein, %	9.9
Digestible Energy, Kcal/g	2.74
Crude Fiber, %	24.3
Digestibility, %	60.2
^a "Fiberite" Aspen sawdust ^b "Pelaid" (Rhodera Inc., Ashland, Ohio) used to enhance pelleting ^c "Mycoban" (Van Waters and Rogers, Anchorage, Alaska) inhibits mold growth	

offered once daily and feed refusals were weighed and subsampled for dry matter determination. Intake was calculated on a daily basis during the trials.

51 Chromium EDTA complex (Cr) was used to mark the liquid phase and 103 ruthenium chloride (Ru) marked particulate phases of the digesta. Ru (2.22×10^{12} dpm/kg BW) was diluted to 2 ml with 10% hydrochloric acid and added to 50 g of the pelleted feed to mark the particulate matter. The amount of feed was selected to prevent altering the pellet structure, when both marking solutions were added. Cr (0.66×10^{12} dpm/kg BW) was diluted to 2 ml with H₂O and added to the previously air dried Ru marked pellets.

Fecal samples were collected opportunistically from observed defecations for 5 days postdosing. Care was taken to prevent contamination from snow and/or particulate matter. Fecal samples were placed in preweighed counting vials and assayed with a dual channel gamma spectrometer. Normal spectral stripping methods were used to calculate marker concentrations, expressed as dpm/g dry matter (Holleman et al. 1983).

Trial Three

In trial 3, 7 adult moose were fed ad libitum with the same pelleted diet used in the 1st experiment. Feed was offered once daily at levels approximately 15% over the

previous week's mean intake to ensure refusals. Orts were collected daily and subsampled for dry matter determination. Intake was calculated on a daily basis.

Cobalt ethylene diaminetetracetic acid (Co) was used as the liquid marker and was prepared as described by Uden et al. (1980). Ytterbium chloride (Yb), the particulate marker, was prepared by soaking the feed with a Yb solution and washing the marked feed with H₂O to remove unbound Yb from the feed (Varga and Prigge 1982). The Yb marked only indigestible materials, and the pelleted structure was destroyed in the soaking and washing process. Soluble materials associated with the pellet structure were lost in the washing. Before dosing, the Yb marked feed was dried at 50C, and fed in the loose form rather than being repelleted. A single dose of 300 g of marked feed (3 g Yb)/moose and 10 g Co/moose was offered together with 300 g unmarked food. The unmarked feed was offered to assist the animal in consuming all the marked feed. If the marked feed was not consumed within 20 min, the marked feed was removed and the animal was not included in the trial.

Fecal samples were collected in T3 as previously described for T1 and T2. Fecal samples were frozen upon collection and thawed immediately prior to analysis. Samples were dried at 50C and ground through a 2 mm screen in a Wiley mill. Dry matter was determined by standard

procedures (AOAC 1980). Analysis of the dried and ground fecal material for Co and Yb was done as described by Hart and Tolan (1984) using acetylene-nitrous oxide flame atomic absorption.

Marker Calculations

All marker concentrations (Ru, Cr, Yb and Co) in fecal material were calculated on a dry matter basis. An interactive computer modeling program using a 2-pool model with 1 time delay was used to generate the 2 exponential components and time delay from fecal excretion curves (Boston et al. 1981).

Calculations of total alimentary fill were based on the rate constants derived in simulation runs of the 2-pool model (Holleman and White 1986).

1) RTT = Rumen turnover times (h)

K_1 = Slope of the fecal excretion descending phase

$RTT = 1/K_1$

2) TMRT = Total mean retention time (h)

K_2 = Slope of the difference between observed and expected marker concentration before equilibration

$TMRT = \text{Transit time} + (1/K_1) + (1/K_2)$

3) VOL = Total fill of digesta (g)

VN = Fill of nondigestible material

DIG = Digestibility

Intake = Intake in g DM/day

$$VN = ((\text{Intake} * (1 - \text{DIG})) / 24) * \text{TMRT}$$

$$\text{VOL} = VN + (VN * \text{DIG}) / (2 * (1 - (\text{DIG})))$$

Statistical Analysis

A simple linear regression program (SPSS/PC 1984) was used for regression analysis. Differences between lines were tested as described by Neter and Wasserman (1974). Wilcoxon test for paired samples was used to test for differences between P-TMRT vs L-TMRT and P-RTT vs L-RTT within a trial (SPSS/PC 1984).

RESULTS AND DISCUSSION

Food Intake

Intake values presented in Table 8 are the means for 14 days (d) spanning 7 d preceding and 7 d postdosing. Ranges in daily intakes (g/kg BW^{0.75}) varied between trials. In T1 intake varied from 45.6 to 62.3 and in T2 from 30.4 to 109.9. This variation was mostly due to the amount of food offered. However, the amount of food intake was not restricted in T3 and ranged from 36.5 to 87.1 (Table 8). The variation in food intake during T3 was probably due to rainy and snowy weather and muddy pen conditions and the fact that animals had been on trial for the previous 4 months.

Table 8. Effect of daily intake ($\text{g/kg BW}^{0.75}$) level on rumen turnover time of particles (P-RTT) and liquid (L-RTT), on total mean retention time of particles (P-TMRT) and liquid (L-TMRT) and digesta volume (VOL) in moose fed a pelleted diet.

<u>Trial 1 (January 1984)</u>						
Animal (kg)	Intake ($\text{g/BW}^{0.75}$)	P-RTT (h)	L-RTT (h)	P-TMRT (h)	L-TMRT (h)	VOL (g)
346	64.6	12.5	10.6	33.8	32.9	5086
383	45.7	34.8	34.4	63.4	63.0	7352
466	55.5	25.7	22.2	47.4	44.8	7689
336	45.6	13.7	12.1	52.3	49.6	5464
466	62.3	22.8	18.9	38.2	35.9	7089
487	55.0	29.5	24.9	47.2	45.9	7547
454	45.7	34.8	32.1	58.3	55.6	7823
<u>Trial 2 (April 1984)</u>						
Animal (kg)	Intake ($\text{g/BW}^{0.75}$)	P-RTT (h)	L-RTT (h)	P-TMRT (h)	L-TMRT (h)	VOL (g)
454	35.9	22.7	22.5	46.3	44.0	4792
477	45.4	30.5	30.2	50.9	46.7	6304
435	30.4	28.8	28.7	62.8	62.1	5212
450	36.9	31.1	23.5	50.2	48.0	5497
345	90.7	21.9	21.8	31.7	30.7	6427
455	36.9	31.7	26.1	51.0	47.6	5241
357	68.7	23.7	25.1	38.9	39.4	6180
463	109.9	24.3	28.0	36.3	36.7	11099
<u>Trial 3 (April 1985)</u>						
Animal (kg)	Intake ($\text{g/BW}^{0.75}$)	P-RTT (h)	L-RTT (h)	P-TMRT (h)	L-TMRT (h)	VOL (g)
413	87.1	29.6	27.6	48.0	45.6	8920
475	39.2	30.2	31.0	49.0	47.4	7519
422	76.4	25.3	30.4	50.7	52.2	10315
420	36.5	33.3	29.5	46.2	50.7	4448
411	38.8	31.3	30.9	46.2	54.	4657
474	64.1	26.3	32.4	53.0	52.5	8005
420	53.0	28.8	28.9	47.4	55.1	8825

Marker Comparison

Trial 3 was designed after analysis of the results from T1 (Jan 1984) and T2 (Apr 1984). Trials 1 and 2 showed that there was no difference between the liquid and particulate digesta flow rates. Unified flow rates between liquids and particulates had not been reported in the literature for domestic livestock.

The experimental protocol from T1 and T2 was examined and I determined that the solid phase marker (Ru) might have migrated from the particulate matter and was flowing with the liquid phase. Trial 3 utilized a particulate marker which had been validated and had shown separation of particulate and liquid flow rates with domestic livestock (Allen 1982, Varga and Prigge 1982). The results from T3 indicate that the liquid and particulate digesta phases move at the same rate. Therefore, I concluded that the particulate marker in T1 and T2 may not have been migrating from the particulate matter to the liquid pool and the data from all 3 trials were utilized in the results.

Particulate Total Mean Retention Time

Many authors have demonstrated a negative correlation of P-TMRT against intake, which is in agreement with these findings for moose in T1 and T2 (Grofum and Williams 1977, Kennedy and Milligan 1978, Mudgal et al. 1982). However, in

T3, increased intake did not significantly alter P-TMRT (Table 9; Fig. 5).

The results in this study show that P-TMRT can change markedly with no change in digestibility. This is substantiated by Schwartz et al. (1986b) in a concurrent study with the same animals used in T1 and T2. They found that changes in intake had no effect on digestibility throughout the winter and spring. However, they reported a significant ($p < 0.01$) effect by month; apparent dry matter digestibilities (DMD) were significantly higher in March (65%) and April (63%) than December (59%), January (59%), and February (57%). These seasonal differences in digestibilities agree with the hypothesis presented in this study and show that P-TMRT can change markedly with no change in digestibility in winter. Furthermore, digestibility in spring was greater and may be due to longer retention time in the alimentary tract.

However, the generally reported interpretation is that a slow P-TMRT increases digestibility when availability is low and should be reevaluated based on the present results. The generalization may only be true for diets of higher potential digestibility. An estimation of alimentary content size would help to confirm or refute this interpretation.

Table 9. Linear regression equations of particulate (P), liquid (L) rumen turnover times (RTT), particulate total mean retention times (P-TMRT), liquid (L-TMRT) and digestive tract volume (VOL; g/animal BW kg) on intake (g/kg BW^{0.75}) (MI) of moose fed a pelleted diet during winter.

Trial 1 (January 1984)

Y	X	n	Regression Equation	r	Sig.
P-RTT ^a	on MI	7	Y=54.047-0.546X	-0.4824	p=0.2729
L-RTT ^b	on MI	7	Y=55.870-0.630X	-0.5563	p=0.1947
P-TMRT	on MI	7	Y=114.405-1.229X	-0.9480	p=0.0012
L-TMRT	on MI	7	Y=111.475-1.209X	-0.9273	p=0.0026
VOL	on MI	7	Y=24.262-0.148X	-0.7900	p=0.0347
P-TMRT	on L-TMRT	7	Y= 2.289+0.991X	-0.9958	p<0.0001

Trial 2 (April 1984)

Y	X	n	Regression Equation	r	Sig.
P-RTT ^a	on MI	8	Y=31.707-0.086X	-0.6222	p=0.0995
L-RTT ^b	on MI	8	Y=26.153-0.007X	-0.0710	p=0.8674
P-TMRT	on MI	8	Y=62.360-0.288X	-0.8547	p=0.0069
L-TMRT	on MI	8	Y=58.721-0.252X	-0.7983	p=0.0175
VOL	on MI	8	Y= 6.216+0.153X	-0.9793	p<0.0001
P-TMRT	on L-TMRT	8	Y=-0.688+1.051X	-0.9865	p<0.0001

Trial 3 (April 1985)

Y	X	n	Regression Equation	r	Sig.
P-RTT ^c	on MI	7	Y=34.459-0.092X	-0.6651	p=0.1021
L-RTT ^d	on MI	7	Y=31.656-0.027X	-0.3512	p=0.4399
P-TMRT	on MI	7	Y=45.260-0.060X	-0.4825	p=0.2728
L-TMRT	on MI	7	Y=54.426-0.058X	-0.3275	p=0.4734
VOL	on MI	7	Y= 4.546+0.227X	-0.8893	p=0.0074
P-TMRT	on L-TMRT	7	Y=49.976-0.026X	-0.0371	p=0.9371

a ¹⁰³Ruthenium Chloride

b ⁵¹Chromium EDTA

c Ytterbium chloride

d Lithium cobalt EDTA

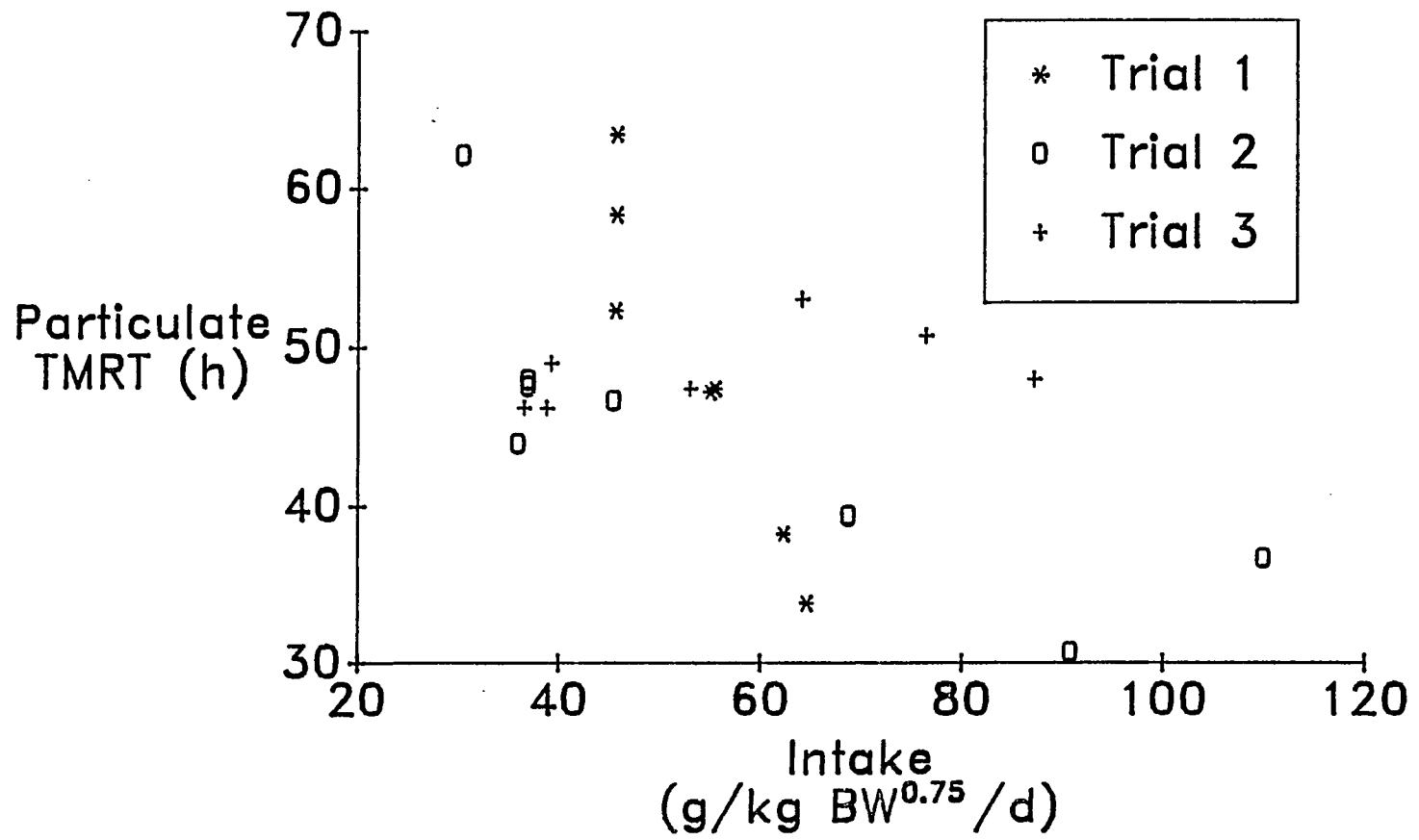


Fig. 5. Particulate total mean retention time (TMRT) related to intake of a pelleted diet. Trial 1 (Jan 1984); Trial 2 (Apr 1984); Trial 3 (Apr 1985).

Liquid Total Mean Retention Time

There was a significant negative correlation between L-TMRT and intake in T1 and T2 (Table 9; Fig. 6). This is in agreement with most reported results with cattle and domestic sheep (Galyean et al. 1979, Adams and Kartchner 1984). In these domestic livestock studies, L-RTT and intake are also inversely correlated as has been reported previously for moose (Hjeljord et al. 1982, Schwartz et al. 1984).

Level of food intake did not affect L-RTT for each of these trials; however, L-RTT for T1 was different from T3 ($p < 0.05$), indicating that rumen liquid pool size and outflow were different. However, a 2nd estimate of either liquid pool size or outflow rate is needed to interpret whether the pool size changes seasonally with food intake.

Retention Time in the Alimentary Tract

Intake had a significant effect on TMRT of both liquid and particle phases in T1, whereas no response to either L-RTT or P-RTT was noted (Table 9). Similarly, in T2 the P-TMRT showed a significant response to intake without a response observed with P-RTT. In T3 no response to intake was observed with either particulate or liquid phases for either RTT or TMRT. Since RTT is suggested to be indicative of rumen turnover time and TMRT represents time spent in the

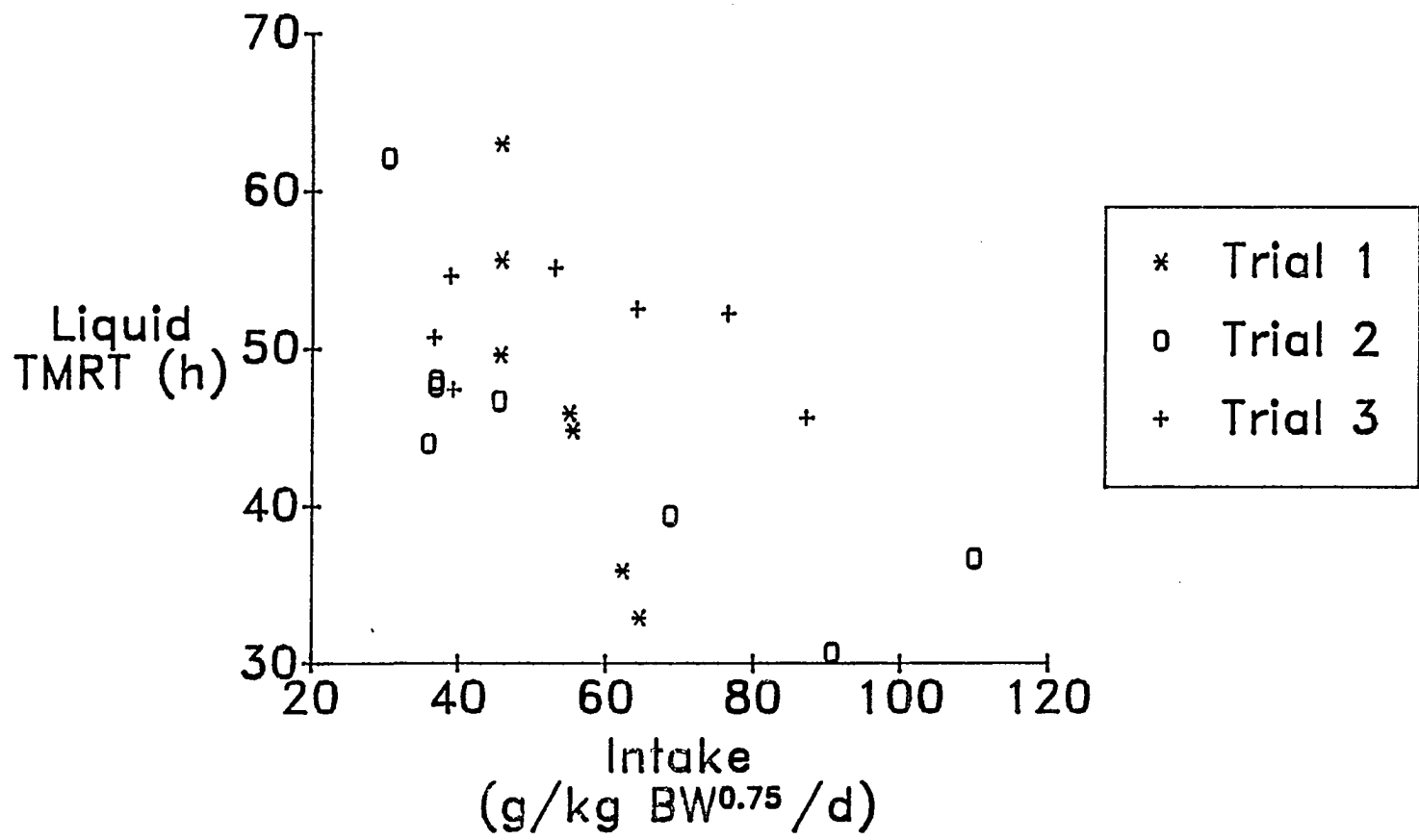


Fig. 6. Liquid total mean retention time (TMRT) related to intake of a pelleted diet. Trial 1 (Jan 1984); Trial 2 (Apr 1984); Trial 3 (Apr 1985).

entire tract, the data suggest that the controlling factor in passage rate through the alimentary tract may not be the rumen, but rather the lower tract as suggested by Faichney and Boston (1983).

The data in Fig. 7 are consistent with the hypotheses that marked particles move with the liquid phases in northern ruminants (White et al. 1984). Most published data with domestic livestock show a distinct separation of particulate and liquid phases in the alimentary tract. The extent of these differences are diet specific and comminution rate greatly affects the measurement of P-TMRT. Reduction of particle size is important when indigestible components of long-fibered, low-quality foods are being digested (Allen 1982).

In the present study, pelleting probably minimized differences between P-RTT and L-RTT, because feed form was mechanically altered (i.e., pelleting) which has a significant effect on animal processing time (Mautz and Petrides 1971, Robbins 1983). The pellets offered a smaller particle size for processing by the animal, thereby reducing rumination time and salivary flow (Church 1975).

Estimation of Alimentary Fill

Provided that the particulate marker reasonably represents the nondigestible component, then an estimate of

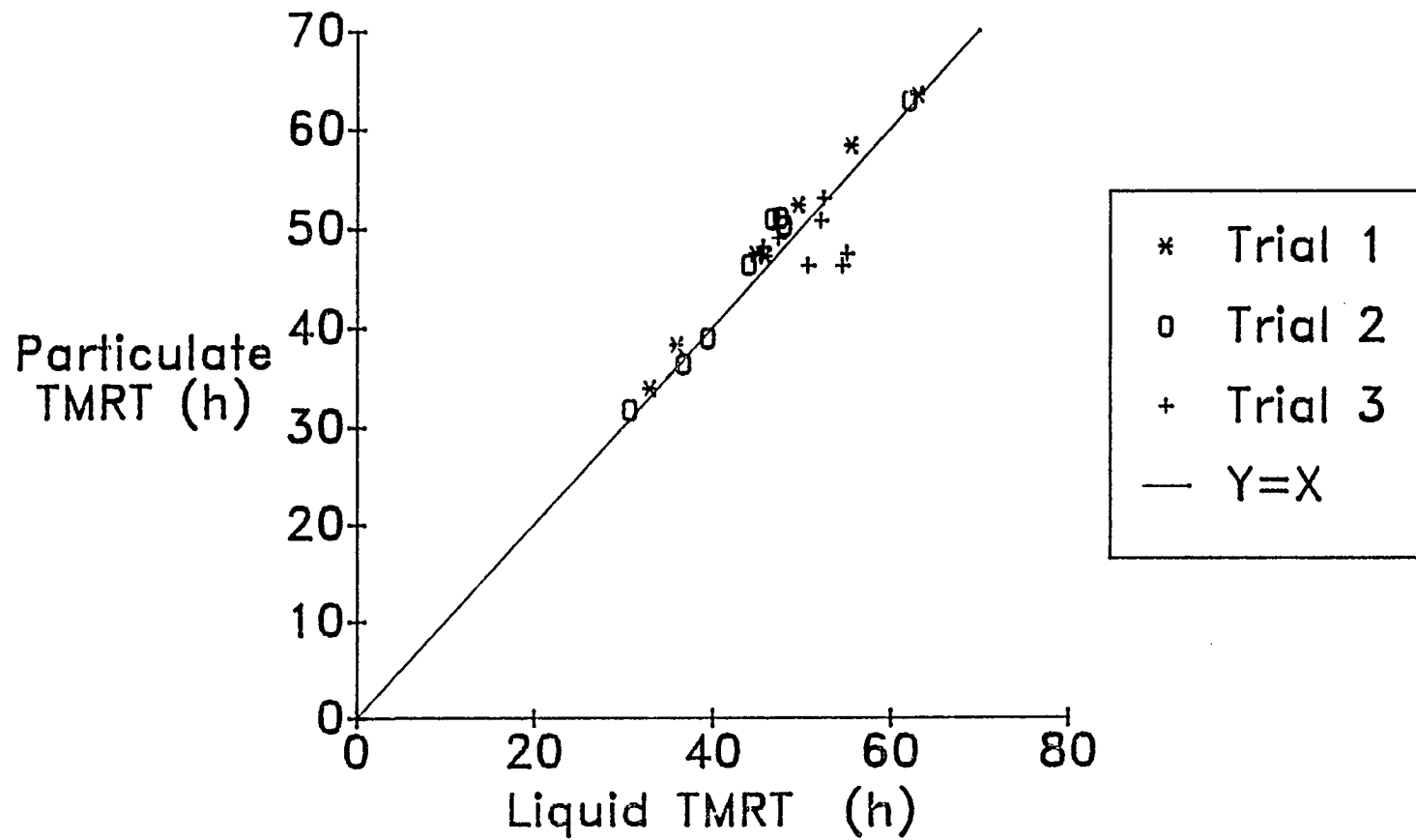


Fig. 7. Particulate total mean retention time (particulate TMRT) on liquid total mean retention time (liquid TMRT) for moose. Trial 1 (Jan 1984); Trial 2 (Apr 1984); Trial 3 (Apr 1985).

the total alimentary fill can be made from estimates of P-TMRT and feces output as proposed by Holleman and White (1986) and shown in Table 8. The regression of VOL/kg BW^{0.75} on food intake (g/kg BW^{0.75}) for T1 tends to constancy whereas in T2 and T3 the range in fill was very large and a significant increase with food intake was noted (Fig. 8; Table 9). These data confirm the hypothesis that during winter (T1) the animal maintains a fairly constant alimentary fill when intake is varied. This process can be interpreted as optimizing the digestibility of diets that are predictably low in winter. Further evidence for this hypothesis could be gained by an analysis of the data of Schwartz et al. (1986b) in which intake changed due to diet digestibility.

In contrast, as spring approaches and food quality is predictably of higher value, alimentary fill becomes adaptable to increasing food supply. This strategy should allow optimization of food digestibility and intake. Thus, P-TMRT would tend to constancy, but would be variable. Relations between P-TMRT and intake are expected to be variably related to intake as shown in T2 and T3 (Table 9).

Interspecies Comparisons of Particulate and Liquid Flows

The relationship between liquid and particulate flow is of interest to the comparative nutritionist because theory

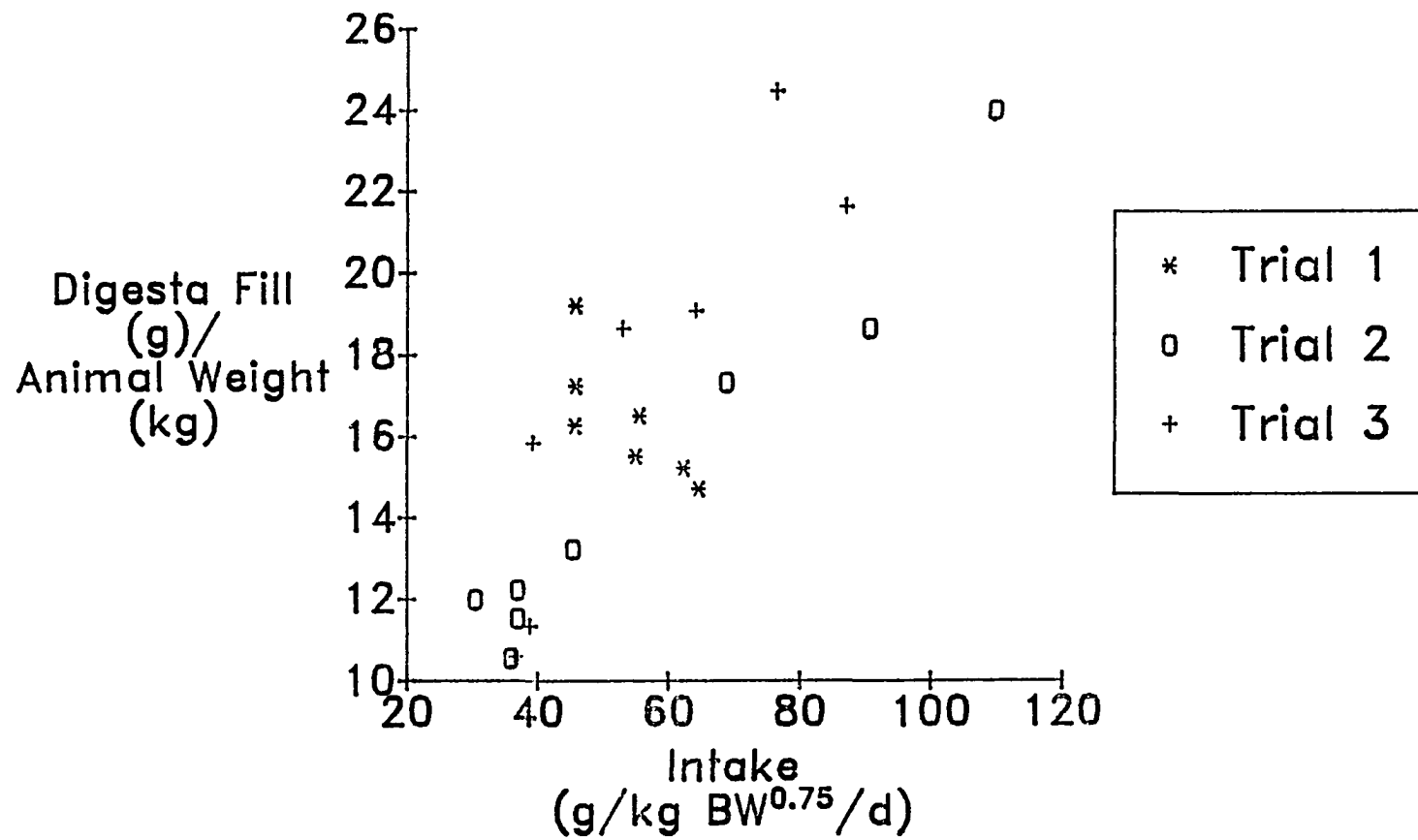


Fig. 8. Alimentary digesta fill/animal weight related to intake of a pelleted diet. Trial 1 (Jan 1984); Trial 2 (Apr 1984); Trial 3 (Apr 1985).

suggests different control mechanisms for browser/concentrate selectors, grazers, and mixed feeders (Kay et al. 1979). RTT data from cattle (Uden et al. 1982, Varga and Prigge 1982) and sheep (Prigge et al. 1984) were compiled for comparison with moose. These studies were selected because diet DMD was between 50-60% (Table 10), and intake changes were due to feeding level rather than digestibility of the feed.

Correlations of L-RTT and P-RTT with intake ($\text{g/kg BW}^{0.75}$) for all species are shown in Table 11. The regressions of P-RTT against intake were not significant for moose, cattle, or sheep. Relationships of L-RTT with intake were variable between species. In sheep a significant ($p=0.006$) correlation of L-RTT against intake was noted. Thus, the handling of the liquid phase in the rumen may be more highly correlated with intake in the browser (moose) than in the grazer (cattle). The trend was also apparent with sheep though it was not significant. Thus, the difference between R-RTT and P-RTT at a given level of food intake was higher in cattle than sheep or moose.

Alternately, the comparison of L-RTT/P-RTT ratio can be used and this ratio was 0.964 for moose, 0.788 for sheep, and 0.395 for cattle. Therefore, the liquid digesta phase in the grazer (cattle) flows at a much faster rate than the solids, whereas in the browser (moose) the differences are

Table 10. Comparison of moose, cattle, and sheep particle (P) and liquid (L) rumen turnover times (RTT; h) with varying levels of intake.

Species	Animal Intake (kg)	(g/kg BW ^{0.75})	P-RTT (h)	L-RTT (h)	L-RTT/P-RTT
MOOSE ^a	345	90.7	21.9	21.8	0.995
MOOSE	455	36.9	31.7	26.1	0.823
MOOSE	357	68.7	23.7	25.1	1.059
MOOSE	463	109.9	24.3	28.0	1.152
MOOSE	413	87.1	29.6	27.6	0.932
MOOSE	435	30.4	28.8	28.7	0.996
MOOSE	450	36.9	31.1	23.5	0.755
MOOSE	411	38.8	31.3	30.9	0.987
MOOSE	420	64.1	26.3	32.4	1.231
MOOSE	474	53.0	28.8	28.9	1.003
MOOSE	346	64.6	12.5	10.6	0.848
MOOSE	466	55.5	25.7	22.2	0.863
MOOSE	477	45.4	30.5	30.2	0.990
MOOSE	454	35.9	22.7	22.5	0.991
MOOSE	454	45.7	34.8	32.1	0.922
MOOSE	420	36.5	33.3	29.5	0.885
MOOSE	336	45.6	13.7	12.1	0.883
MOOSE	487	55.0	29.5	24.9	0.844
MOOSE	466	62.3	22.8	18.9	0.828
MOOSE	475	39.2	30.2	31.0	1.026
MOOSE	422	76.4	25.3	30.4	1.201
MOOSE	383	45.7	34.8	34.4	0.988
CATTLE ^b	610	74.0	37.0	13.5	0.364
CATTLE ^b	610	74.0	50.0	15.6	0.312
CATTLE ^c	405	87.4	22.0	8.0	0.363
CATTLE ^c	405	86.1	28.1	10.4	0.370
CATTLE ^c	405	53.5	23.9	13.3	0.556
CATTLE ^b	260	53.8	31.3	16.4	0.523
CATTLE ^b	220	51.7	45.5	15.9	0.349
CATTLE ^b	450	68.6	55.6	16.4	0.294
CATTLE ^c	405	51.0	28.1	11.8	0.419
SHEEP ^c	46	62.2	20.2	10.6	0.524
SHEEP ^c	46	51.8	15.1	10.4	0.688
SHEEP ^d	27	41.7	18.2	32.3	1.774
SHEEP ^d	27	33.5	19.2	27.8	1.447
SHEEP ^d	46	84.1	15.2	8.7	0.572
SHEEP ^d	27	70.5	15.2	14.1	0.927
SHEEP ^d	27	57.0	15.2	13.7	0.901
SHEEP ^c	46	49.1	19.0	13.7	0.721
SHEEP ^b	31	52.7	27.0	19.2	0.711
SHEEP ^b	34	54.0	47.6	17.5	0.367

Table 10. Continued.

Species	Animal (kg)	Intake (g/kg BW ^{0.75})	P-RTT (h)	L-RTT (h)	L-RTT/P-RTT
SHEEP ^b	25	50.0	47.6	20.8	0.436
SHEEP ^b	33	53.6	50.0	18.9	0.378

- a Present study
 b Uden et al. 1982
 c Prigge et al. 1984
 d Varga and Prigge 1982

Table 11. Comparison of particle (P), liquid (L) rumen turnover times h/kg BW^{0.25} (RTTW), and L-RTT/P-RTT (Ratio) with 3 ruminant species fed varying levels of intake g/kg BW^{0.75} (INT) of diets ranging from 50 to 56% digestibility.

<u>Moose</u>				
Y on X	n	Y = a + bX	r	Sig.
P-RTTW on INT	22	Y=7.07-0.021	-0.343	p=0.119
L-RTTW on INT	22	Y=6.00-0.005	-0.080	p=0.722
L-RTT on P-RTT	22	Y=1.95+0.891	0.852	p=0.001
Ratio on INT	22	Y=0.82+0.003	0.426	p=0.482
<u>Cattle</u>				
Y on X	n	Y = a + bX	r	Sig.
P-RTTW on INT	9	Y=10.74-.041	-0.224	p=0.563
L-RTTW on INT	9	Y=5.47-0.037	-0.683	p=0.043
L-RTT on P-RTT	9	Y=6.93+0.183	0.748	p=0.021
Ratio on INT	9	Y=0.61-0.003	-0.534	p=0.139
<u>Sheep</u>				
Y on X	n	Y = a + bX	r	Sig.
P-RTTW on Int	12	Y=14.99-.079	-0.178	p=0.580
L-RTTW on Int	12	Y=17.47-.185	-0.728	p=0.007
L-RTT on P-RTT	12	Y=14.48-.110	0.216	p=0.500
Ratio on Int	12	Y=1.72-0.017	-0.509	p=0.091
Species	n	L-RTT/P-RTT (mean)	(SD)	Range
Moose	22	0.964 ^a	0.1230	0.7556 - 1.2319
Cattle	9	0.395 ^b	0.0900	0.2950 - 0.5565
Sheep	12	0.787 ^{a,b}	0.4312	0.3676 - 1.7747

^a Different letters within a column denote a significant difference (p<0.05) using Scheffe test for differences.

small (Fig. 9). A selective advantage for separation of liquid from particulate flow may be dependent on forage selection.

CONCLUSIONS

Moose have an adaptive digestive strategy to optimize forage energy intake. Diet quality for moose varies greatly from summer to winter (Oldemeyer and Regelin 1986). The winter diet consists mainly of highly lignified woody browse while the summer diet is made up of highly digestible vascular material. These 2 different types of plant material have different rates of digestion (Spalinger 1985). Woody browse has a highly lignified cortex covered with a more digestible outer surface (Oldemeyer and Regelin 1986, Spalinger 1985). For the moose to optimize winter forage energy intake it must digest the bark and rapidly pass the cortex through the digestive tract. However, if forage availability is limited, then slowing the rate of passage would be beneficial and allow for digestion of the woody browse cortex.

Moose have a winter digestive strategy that optimizes forage energy intake by altering passage rate to maintain a constant alimentary fill. This allows rapid movement of low digestible portions of the diet through the alimentary tract

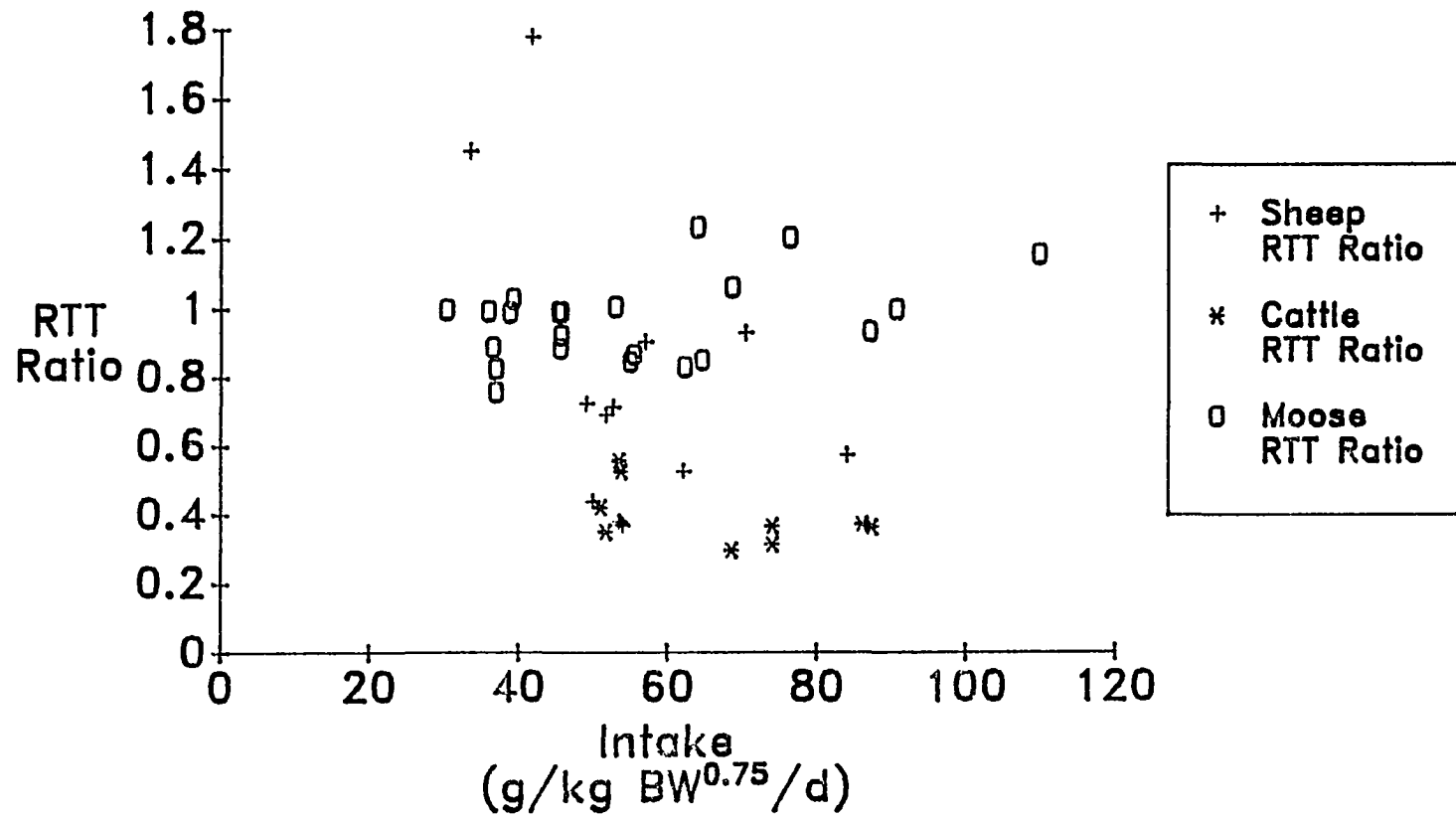


Fig. 9. Liquid rumen turnover time divided by particulate rumen turnover time (RTT Ratio) against intake of diets between 50 and 60% digestibility.

and also allows longer retention times during periods of low forage intake.

In spring and summer, the highly vascular plant material eaten by moose is digested rapidly (Spalinger 1985), so that increased retention time in the alimentary tract is not beneficial. Because spring and summer forage is seldom limiting (Oldemeyer and Regelin 1986), the moose can increase energy intake by increasing alimentary fill of the highly digestible forage.

CHAPTER 3

INFLUENCE OF ENERGY INTAKE ON RESTING METABOLISM OF MOOSE

INTRODUCTION

Basal metabolic rate (BMR) represents the minimal energy expenditure to support life (Kleiber 1975). Classically, it has been estimated as the heat production of the resting animal in the postabsorptive state in a thermo-neutral environment. This is frequently termed standard fasting metabolism (SFM) and empirical measurements indicate an allometric relationship with body weight (BW,kg) to the 0.75 power (Kleiber 1975). For SFM in eutherian mammals, the empirical measure of BMR is $70 \text{ kcal/kg BW}^{0.75}/\text{d}$; however, within a species the allometry is often different from 0.75 (Robbins 1983). Thus, the allometry of BMR is a broad generalization with many species lying above and below the standard value of 0.75. Larger wildlife species are usually above this line with much of the variation attributed to seasonal differences in SFM (white-tailed deer, Odocoileus virginianus, Silver et al. 1969; caribou, Rangifer tarandus, McEwan and Whitehead 1970; roe deer, Capreolus capreolus, Weiner 1977; moose, Alces alces, Regelin et al. 1985).

In species other than man, confusion surrounds both the BMR-SFM terminology and the protocol for estimation of BMR. Empirically defined conditions are difficult to attain with

wildlife species. Wild animals vary greatly in their tolerance to confinement and therefore may not lie quietly in the metabolism stall. Furthermore, any requirement of fasting with ruminants lends itself to error because different levels of food intake, body size, and food passage rate alter the time required until the postabsorptive state is reached (Marston 1948, Blaxter 1962, Kleiber 1975).

Kleiber (1975) suggested that measurement of SFM should take place following a prolonged period of feeding at maintenance levels. Wild ruminants are in a constant flux, gaining and losing weight seasonally, and a component of the change is of endogenous origin (McEwan and Whitehead 1970). Therefore, wild ruminants are virtually impossible to maintain at a constant weight or intake, except during early winter. Heat production measurements at other than the winter period are seldom done at maintenance. Most estimations of SFM with wild ruminants have been made with animals fed ad libitum (Silver et al. 1969, Pauls et al. 1981, Regelin et al. 1985). Seasonal estimates of SFM with moose fed ad libitum vary from a winter low of 76 to a summer high of 143 kcal/kg $W^{0.75}$ /d (Regelin et al. 1985). This seasonal difference in SFM is consistent with most reported results with other wild ruminants fed ad libitum (Silver et al. 1969, Pauls et al. 1981).

An estimate of BMR independent of seasonal weight and intake dynamics is needed. Such an estimate would determine if seasonal variation in fasting metabolism was due to the plane of nutrition or a seasonal endogenous change in BMR.

Resting metabolism (RM) is the heat produced by an animal while in a lying, fed state. This estimate of heat production is the summation of BMR and heat increment. Including heat increment reduces the error associated with the variable time required to achieve a postabsorptive state in ruminants.

An objective of this study was to investigate the influence of metabolizable energy intake (MEI; kcal/kg $BW^{0.75}$ /d) on resting metabolism in moose. Reid and Robb (1971) advocated extrapolating heat production to zero MEI to obtain an estimate of theoretical basal metabolism (TBM). Estimation of TBM will be a second objective of this study and TBM will be used to evaluate seasonal differences in BMR.

MATERIALS AND METHODS

The study was conducted at the Moose Research Center on the Kenai Peninsula of Alaska during winter and spring 1984-85. Nine adult moose were evenly allotted into 3 dietary treatments with metabolizable energy (ME) content of 1.99, 2.26, and 2.61 kcal/g dry matter (Table 12).

Table 12. Composition (% D.M. basis) of a high-quality (HQ), medium-quality (MQ), and low-quality (LQ) ration fed to moose at the Moose Research Center Kenai Peninsula, Alaska, winter 1984-85.

Constituent	HQ	MQ	LQ
Corn	28.7	27.6	26.4
Sawdust ^a	25.9	24.8	23.6
Oats, rolled	17.2	8.6	0.0
Soybean meal	7.2	6.4	5.5
Cane molasses	5.7	6.6	7.5
Barley	5.7	2.9	0.0
Beet pulp	5.7	2.9	0.0
Rice hulls	0.0	17.1	34.1
Vitamin Premix	0.3	0.2	0.1
Dical ^b	1.3	1.2	1.1
Pelaid ^c	1.4	1.4	1.3
Nutritional Content			
Crude protein (%)	9.85	8.38	6.9
Metabolizable energy (kcal/g)	2.61	2.26	1.99
Crude fiber %	24.3	29.5	34.8
Digestibility (%)	53.1	47.8	43.8

^a "Fiberite" commercial aspen sawdust

^b Dicalium phosphate

^c "Pelaid" (Rhodera Inc. Ashland, Ohio) used to enhance pelleting

Composition of the medium quality (MQ) and low quality (LQ) rations were based on dilution of the high quality (HQ) ration with rice hulls, and supplied 85% and 70% of the ME and crude protein (CP), respectively. Crude fiber (CF) content of the MQ and HQ rations were respectively 85% and 70% of the LQ diet.

All rations were fed ad libitum with feeding levels adjusted weekly to assure 15% daily refusals. Feed was offered once daily and refusals were weighed and subsampled for dry matter determination. Animals were individually housed in open 3 X 10 m pens with access to water and trace mineralized salt at all times.

Estimation of Resting Metabolism

Resting metabolism was estimated using an open circuit respiration chamber described by Regelin et al. (1985). The air stream leaving the chamber was monitored for CO₂, O₂, and CH₄. All volume measures were adjusted to standard temperature and pressure (Regelin et al. 1981). Heat production was calculated by multiplying the volume of O₂ consumed during the trial by the thermal equivalent of O₂ at the extant respirator quotient. Heat production was expressed as kcal/kg BW^{0.75}/d (Regelin et al. 1985).

The respiration chamber was located near human and moose activities. To reduce the effects of these

disturbances, animals entered the chamber approximately 1 h before sunset. All moose used in the trial had been previously acclimated to confinement in small quarters. Feed and water were available immediately prior to entering the chamber, but only water was available in the respiration chamber.

The animals' activity was monitored constantly during the 8 h maximum time limit for the trial. Fig. 10 depicts estimated heat production during a typical experiment, with the animal entering the chamber at time 0. Animals usually stood until they became relaxed in the chamber, causing heat production to increase from time 0 to 105 min. In the trial shown in Fig. 10, the moose lay down at 105 min and heat production decreased; however, there is a lag time associated with the chamber volume and flow through the chamber. Since gas concentration measurements reflect air leaving the chamber rather than the animal, care was taken to allow the chamber to equilibrate after any change of oxygen consumption by the animal. Estimation of heat production began at 195 min in this example. Heat production was estimated constantly and pooled in 15 min samples to adjust for rapid fluctuations. The trial was terminated once 3 consecutive 15-min heat production estimates were completed without further decrease or increase in heat production and a coefficient of variation of less than 8% was observed.

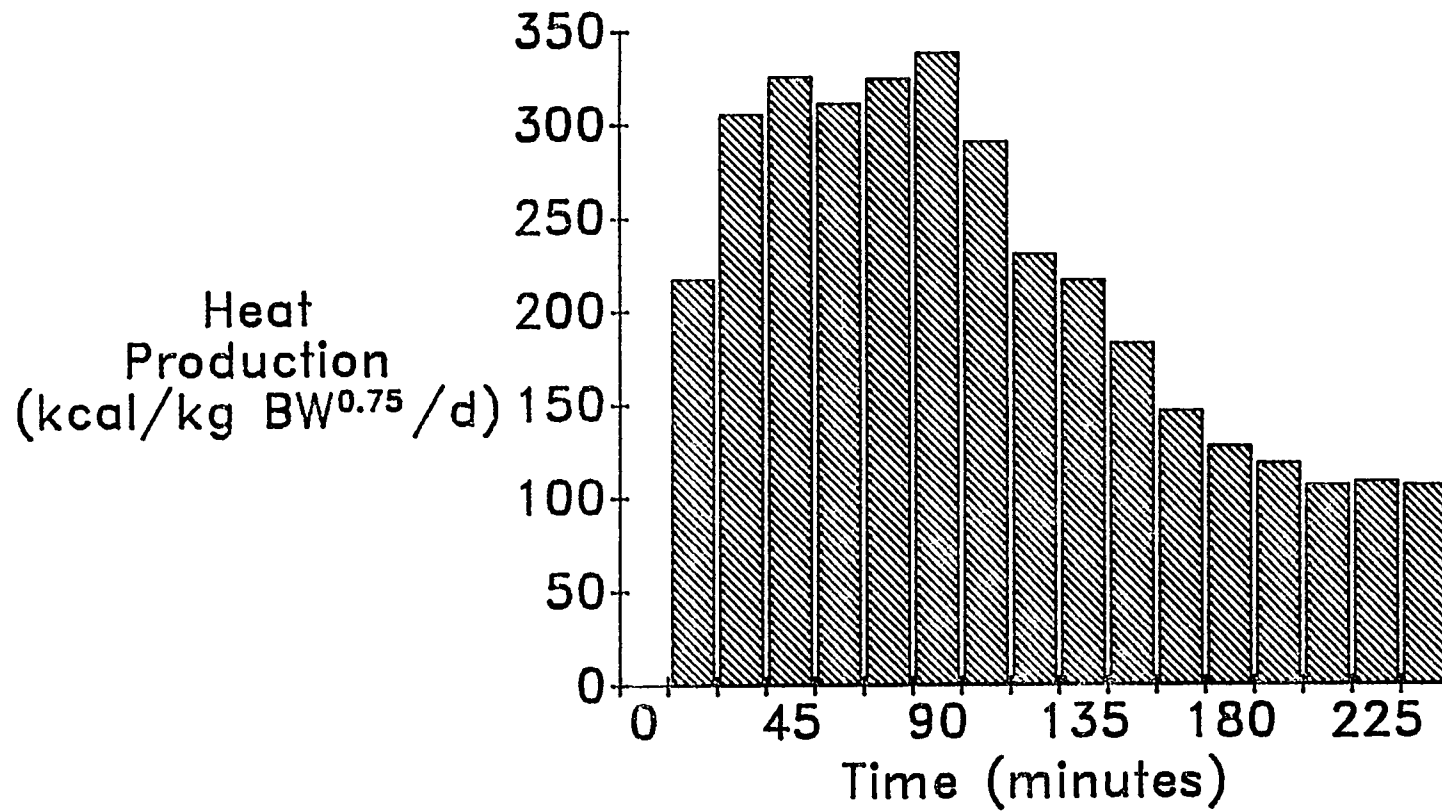


Fig. 10. Example of heat production of a moose in an open circuit respiration chamber by time.

If an animal stood during a trial, estimation of heat production was terminated and restarted once the animal was lying again for 90 min. Estimates of heat production were made on December 23-31 (T1), February 16-24 (T2), and April 16-20 (T3). Each trial was completed within a 9-day period.

Statistical Analysis

Simple linear and multilinear regression analysis was done using Statgraphics (1985). Testing of differences between 2 lines was done as described by Neter and Wassermann (1974). One-way analysis of variance was used to test for differences between trials (SPSS/PC 1984), and differences were tested by a Scheffe test ($p < 0.05$).

RESULTS AND DISCUSSION

Plane of Nutrition

During the 3 trials, intake of dry matter ($\text{g/kg BW}^{0.75}/\text{d}$) was significantly different among the 3 treatments. The animals on the LQ and MQ rations had a higher intake than animals on the HQ diet. Furthermore, the animals on the LQ diet consumed significantly more than animals on the MQ ration (Table 13). However, intake of metabolizable energy ($\text{kcal/kg BW}^{0.75}/\text{d}$) was not significantly different among the 3 rations (Schwartz et al. 1986b). The moose altered dry matter intake of the different quality diets to maintain a

Table 13. Effect of a high-quality (HQ), medium-quality (MQ), and low-quality (LQ) ration on seasonal intake of dry matter (INTAKE) (g/kg BW^{0.75}d) and metabolizable energy intake (ME) (kcal/kg BW^{0.75}/d) in moose during winter 1984-85 at the Moose Research Center, Kenai Peninsula, Alaska.

Variable	n	INTAKE	SD	ME	SD
Trial 1 (December 23-31)					
HQ	3	52.7	10.95	137.7	28.57
MQ	1	64.7	-	146.3	-
LQ	3	82.4	3.45	164.0	6.86
Pooled	7	67.2	16.26	150.2	21.52
Trial 2 (February 16-24)					
HQ	3	53.2	12.69	138.9	33.11
MQ	1	68.6	-	155.0	-
LQ	3	74.8	13.15	148.8	26.17
Pooled	7	64.7	15.19	145.4	25.23
Trial 3 (April 16-20)					
HQ	2	52.3	10.04	136.6	26.21
MQ	1	65.4	-	147.8	-
LQ	3	79.6	7.39	158.4	14.70
Pooled	6	68.2	14.9	149.4	18.39
Pooled by Treatment					
HQ	8	52.8 ^a	9.73	137.9a	25.40
MQ	3	66.2 ^b	2.06	149.7a	4.66
LQ	9	78.9 ^c	8.43	157.1a	16.77
Grand mean	20	66.6	14.73	148.3	21.00

^a Different letters within a column denote significant differences ($p < 0.05$) by Scheffe test.

relatively constant MEI among the 3 treatments. Therefore, the plane of nutrition was similar on all 3 treatments.

To test the hypothesis that current and previous level of MEI ($\text{kcal/kg BW}^{0.75}/\text{d}$) affects metabolic rate, a step-wise regression analysis of RM on MEI was used (Koong et al. 1985). MEI was calculated for the previous 7, 14, 21, 28, and 35 days before the RM measurement. RM was correlated with previous MEI time intervals for each of the 3 trials and for the pooled data. In all analyses the highest correlation of RM on MEI was with the previous 28 d mean ($p < 0.01$). Therefore, in all subsequent analysis the previous 28 d mean metabolizable energy intake (P28D) was used. These results suggest that metabolic adjustment to the level of intake is a long-term process and supports the hypothesis that cellular metabolism adapts to substrate supply slowly and therefore takes a considerable time to return to basal or reference level of heat production.

Theoretical BMR

Theoretical BMR or true basal metabolism (TBM) is the intercept of the regression of RM (Y) on MEI (X). At the intercept, the heat production estimate does not include heat produced from the digestion of feed (i.e., heat increment) (Reid and Robb 1981), and therefore is an estimate of the minimal heat production. The zero-intake intercepts

in this study were 68.8, 55.4, and 81.3 kcal/kg BW^{0.75}/d for trials 1, 2, and 3, respectively (Fig. 11; Table 14). The pooled mean of 68.8 kcal/kg BW^{0.75}/d is almost identical to the inter-species estimate of BMR (70 kcal/kg BW^{0.75}/d) (Kleiber 1975).

T3 was conducted during April, when moose are undergoing behavioral changes and are adapting to dietary changes. The intercept of 81.3 kcal/kg BW^{0.75} was higher than the December and February estimates of TBM of T1 (68.8) and T2 (55.4 kcal/kg BW^{0.75}/d). Though the differences among the trials appeared large, the differences were not significant ($p < 0.05$).

Nilssen et al. (1984) reported that RM of standing reindeer increased with food intake and that summer estimates of RM were 60 to 72% higher than winter values. They further showed that there was no correlation of thyroid hormones with RM. The zero-intake intercept shows a TBM estimate of 72 which is comparable with our pooled estimate of 68.8 (kcal/kg BW^{0.75}/d).

Marston (1948) was the first to show that the level of MEI increased RM. This was confirmed by Graham et al. (1974) and Graham and Searle (1975), but not by Drew and Reid (1975). The latter study was made after food deprivation and reflects compensatory or catch-up growth, suggesting a change in metabolic efficiency. A recalculation of Marston's

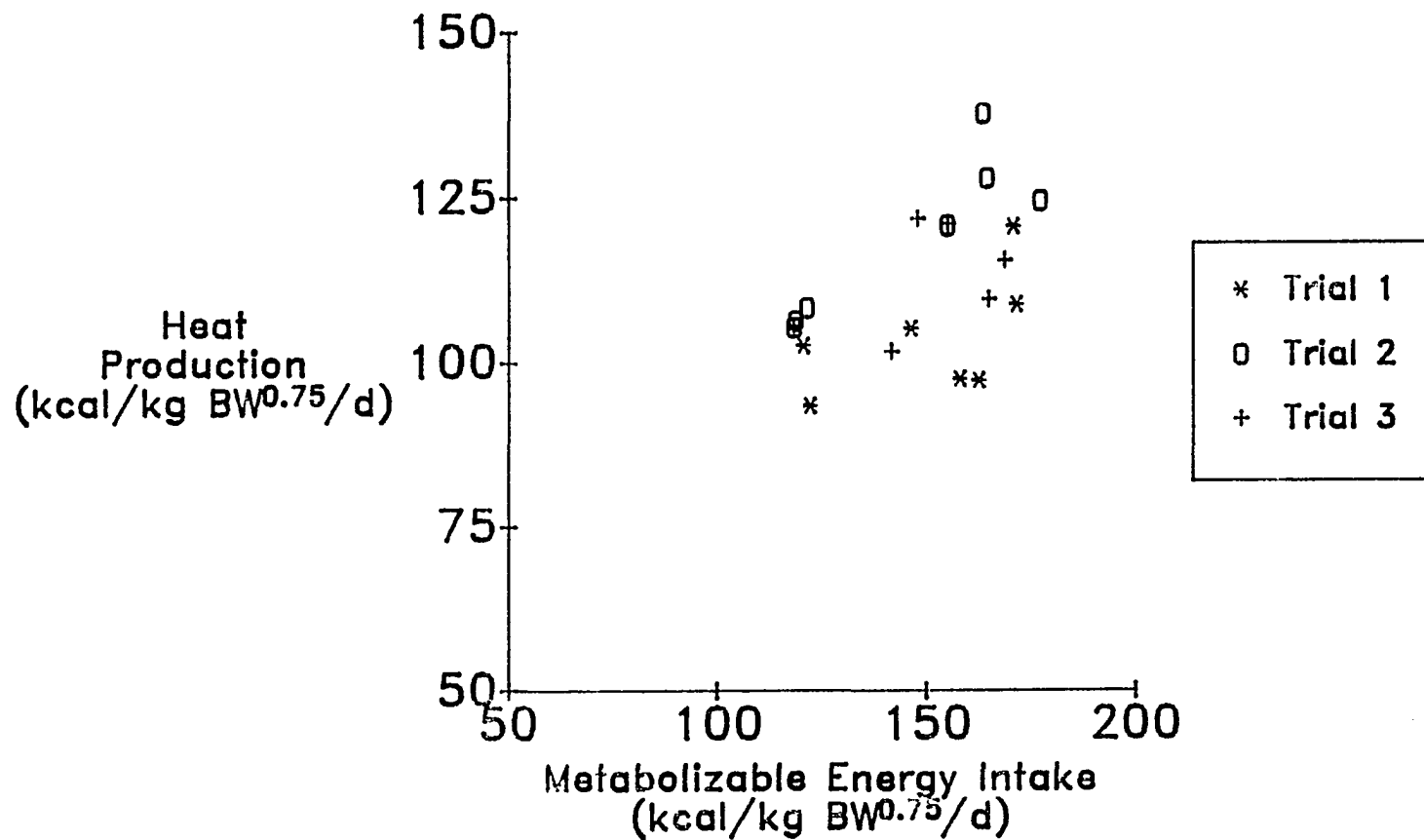


Fig. 11. Heat production and metabolizable energy intake for moose. Heat production was estimated for a lying, fed moose using an open circuit respiration chamber. Metabolizable energy intake is the mean of the previous 28 d. Dec 1984 (T1), Feb 1985 (T2), and Apr 1985 (T3).

Table 14. Linear regression equations of resting metabolism (RM) (Y) on previous 28-day mean metabolizable energy intake (X) (kcal/kg BW^{0.75}/d) for moose, Moose Research Center, Kenai Peninsula, Alaska, winter 1984-85.

Trial	n	Intercept	(SE)	Slope	(SE)	r	Prob.
1	7	68.8	24.09	0.232	0.1590	0.547	p=0.204
2	7	55.4	15.01	0.435	0.1019	0.886	p=0.008
3	6	81.3	29.95	0.209	0.1992	0.465	p=0.353
Pooled	20	68.8	16.64	0.289	0.1111	0.522	p=0.018

data, regressing RM on MEI, shows a TBM of 55.6 which is not significantly lower than the TBM of 68.8 kcal/kg BW^{0.75}/d for moose reported in this paper (Table 14). Reid and Robb (1971) stated that the TBM of cattle is usually between 38 and 56, and Forbes et al. (1928 as cited by Marston 1948) reported TBM for cattle being 51.9 kcal/kg BW^{0.75}/d. These estimates of BMR in domestic animals are significantly lower than the classical inter-species estimate of 70 kcal/kg BW^{0.75}/d (Kleiber 1975). The values obtained with moose are slightly higher than those for cattle and domestic sheep and support the often reported hypothesis that wild ruminants have higher metabolic rates.

Efficiency of Energy Utilization

The intercept of the regression of RM on MEI gives an estimate of TBM; the slope of this line is an estimate of heat increment. The slope represents the unit loss of heat/unit increase in MEI. The slopes of the lines produced from data in T1, T2, and T3 were not significantly different, suggesting no changes in efficiency with the seasonal change from winter to spring. The efficiency with which ME is retained is given by 1-slope (i.e., 1- 0.289= 0.711). Since these animals are essentially at maintenance or below, the efficiency is equivalent to km of the ARC (1980) system, which for this diet is predicted to be 0.69

and is in excellent agreement with the 0.71 observed in this study.

Body Condition

Body condition, particularly the fat reserves of an animal, may also affect maintenance and BMR independent of plane of nutrition and endogenous rhythm effects. The effects of body condition on BMR were examined by Reid and Robb (1971). These authors recalculated estimates of maintenance requirements and efficiency of metabolism in fat and thin steers generated by Armsby and Fries (1917 cited by Reid and Robb 1971). The regression equation of daily energy balance (kcal/kg BW^{0.75}/d) on daily MEI for thin steers was $Y = -64.2 + 0.604X$, and for fat steers $Y = -68.7 + 0.568X$.

Since heat production = MEI - energy balance (Lofgreen and Garrett 1968) the regression equations for fat and thin steers can be converted from:

$$\text{(thin steer) } Y = -64.2 + 0.604X \text{ to } Y = 64.2 + 0.396X$$

$$\text{(fat steer) } Y = -68.7 + 0.568X \text{ to } Y = 68.7 + 0.432X$$

The equations are now comparable with my pooled equation for moose $Y = 68.8 + 0.289X$.

The intercepts for the thin steer, fat steer, and moose are similar, 64.2, 68.7, and 68.8 kcal/kg BW^{0.75}/d,

respectively, though the thin steer has a TBM slightly less than the moose or the fat steer.

Differences in BMR and energy retention efficiency tend to have a multiplicative effect when one estimates food requirements or production (White 1983). Ruminants indigenous to seasonal environments (i.e., dry tropics, northern temperate, and arctic environments) are required to survive on body reserves of fat during periods of low forage quality and availability. Therefore, wild ruminants are constantly fluxing between catabolism and anabolism of fat and lean tissue. The seasonality of wild ruminants complicates determination of maintenance requirements and estimation of BMR.

Respiratory Quotient

Respiratory quotient (RQ) was regressed on RM and MEI with no significant correlations (Fig. 12). However, a significant difference ($p < 0.05$) was noted between the mean RQ values in T2 (0.62) and T3 (0.78) (Table 15). Trial 2 coincided with a seasonal period of voluntary weight loss and voluntary reduction in food intake (Schwartz et al. 1984).

The lowest seasonal RQ of 0.62 is outside the normal range of 0.7 to 1.0. A RQ of 0.7 indicates fat combustion which would agree with the status of animals in midwinter

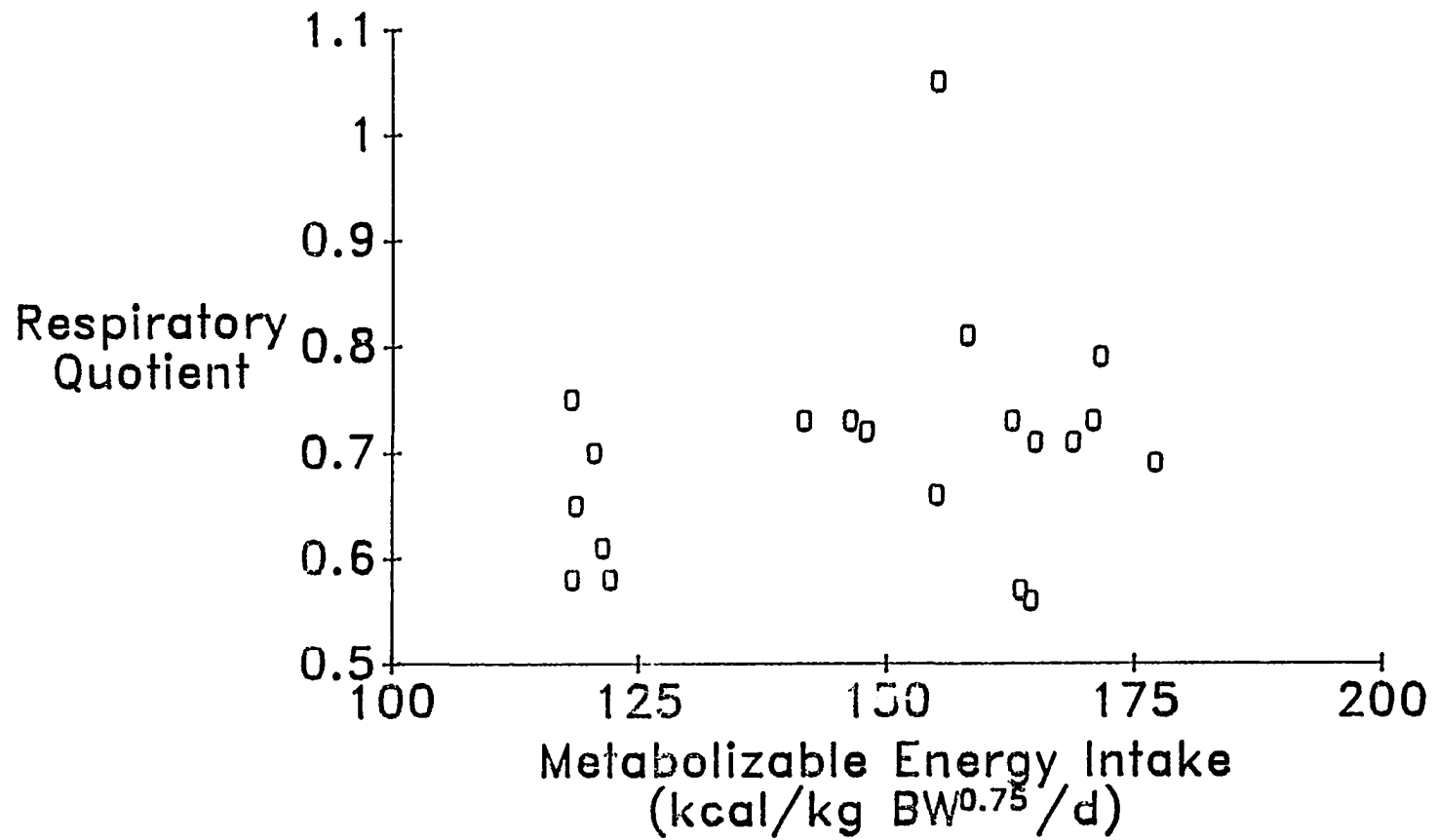


Fig. 12. Relation of respiratory quotient and metabolizable energy intake for moose.

Table 15. Resting metabolism (RM), respiratory quotient (RQ), and previous 28-day metabolizable energy intakes (P28D) (kcal/kg BW^{0.75}/d) by animal (BW,kg) and treatment (TRT). Trials were conducted at the Moose Research Center, Kenai Peninsula, Alaska, winter 1984-85.

Trial 1 (December 23-31)							
Animal	BW	Trt	RQ	SD	RM	SD	P28D
1	477	LQ	0.81	0.017	97.5	2.28	158.0
2	426	LQ	0.79	0.005	108.8	2.49	171.4
3	431	LQ	0.73	0.011	97.3	1.24	162.5
4	416	MQ	0.73	0.014	105.2	0.96	146.3
5	419	HQ	0.58	0.009	93.4	2.42	122.0
6	465	HQ	0.70	0.011	102.6	1.87	120.4
7	410	HQ	0.73	0.013	120.6	1.93	170.7
Pooled	435	(25.8)	0.72 ^{a,b}	0.074	103.6	9.13	150.2
Trial 2 (February 16-24)							
Animal	BW	Trt	RQ	SD	RM	SD	P28D
1	439	LQ	0.65	0.005	106.3	1.24	118.6
2	431	LQ	0.57	0.007	137.7	1.36	163.4
3	422	LQ	0.56	0.012	127.8	2.27	164.4
4	414	MQ	0.66	0.005	120.7	0.72	155.0
5	406	HQ	0.58	0.009	105.3	1.11	118.2
6	460	HQ	0.61	0.006	108.3	1.46	121.3
7	415	HQ	0.69	0.007	124.4	1.89	177.0
Pooled	427	(18.4)	0.62 ^a	0.050	118.6	12.39	145.4
Trial 3 (April 16-20)							
Animal	BW	Trt	RQ	SD	RM	SD	P28D
1	417	LQ	0.73	0.002	101.7	1.43	141.6
2	427	LQ	0.71	0.004	115.6	1.85	168.7
3	407	LQ	0.71	0.007	109.6	2.34	164.8
4	425	MQ	0.72	0.003	121.8	1.45	147.9
5	413	HQ	-	-	-	-	-
6	475	HQ	0.75	0.003	105.5	0.54	118.1
7	416	HQ	1.05	0.005	121.0	2.60	155.1
Pooled	428	(24.2)	0.78 ^b	0.134	112.5	8.28	149.4

^a Different letters within a column denote significant differences ($p < 0.05$) by Scheffe test.

(T2; February). However, RQ's below 0.7 have been reported for animals which are accumulating CO₂, or preferentially metabolizing long chain fatty acids. During T3, animal number 7 had an RQ in excess of 1.0 indicating a shift to carbohydrate combustion, lipid synthesis from volatile fatty acids, or CO₂ depletion (Kleiber 1975).

CONCLUSIONS

The use of regression analysis of resting metabolism on metabolizable energy intake not only provided estimates of TBM but also estimates of efficiency of energy utilization. The TBM for moose was 68.8 kcal/kg BW^{0.75}/d which is slightly higher than values reported for cattle (51.9) and domestic sheep (55.6). This technique also provided an estimate of the efficiency of metabolizable energy retention (71%) for moose.

The TBM in April appeared higher (81.3; SE=30.0) than in January (68.8; SE=24.1) or February (55.4; SE=15.0); however, the differences were not significant.

Simulation modeling of animal production systems are becoming widespread throughout biological sciences. The classical approach reported by Regelin et al. (1985) suggests formulating requirements on an additive model based on BMR, heat increment, and storage which is inherently prone to uncertainty of the BMR estimate. The formulation

of an energy model based solely on empirical knowledge of resting metabolism and MEI would overcome the uncertainty of the additive model as used by numerous workers (see review by Hudson and White 1985).

CHAPTER 4

SIMULATION OF FOOD INTAKE AND ENERGETICS

INTRODUCTION

Concepts of Carrying Capacity

Carrying capacity (CC) has been defined in various ways (MacNab 1985) but is traditionally defined as the propensity for a unit of land to support a unit of animals for a unit of time (Stoddard et al. 1975). CC does not address the condition or quality of the individuals. Determination of CC requires not only an understanding of animal energy partitioning but also forage availability, forage quality, diet selection, animal behavior, and many other ecological and biological factors.

Within recent years, several authors (Moen 1973, Robbins 1973, Wallmo et al. 1977) have advocated determining CC for wild ungulates on a nutritional basis. The estimation of food intake is paramount to predicting forage utilization, to understanding grazing strategies, and ultimately to estimating the CC of the range.

However, measurement of food intake is difficult to obtain under natural conditions. Furthermore, determination of what animals will eat of the available herbage may change under different density levels and snow depth. Therefore, simulation models have been employed to generate estimates

of forage utilization under various conditions and to predict CC (Hobbs et al. 1982, Hobbs and Swift 1985, Hudson and White 1985).

Factors Regulating Intake

Because prediction of food intake is paramount to predicting CC, an understanding of the factors controlling food intake must be understood.

Food intake may be controlled physically by the capacity of the digestive tract and/or physiologically by the end-products of digestion. Both mechanisms are implemented and integrated through the central nervous system (Forbes 1980). Baumgardt (1970) proposed and Ammann et al. (1973) demonstrated for white-tailed deer that regulation of food intake changes from primarily physical (i.e., bulk limited) to physiological (i.e., caloric or self limited) as food nutritive value increases.

Foods of low nutritive values limit gastrointestinal capacities and passage rates which cause feeding bouts to terminate before the animal's energy requirements are met. As nutritive value increases, the animal is ultimately able to ingest enough food to meet its energy requirements, and end products of digestion may not only terminate the feeding bout but may also delay the onset of the following feeding bout. Therefore, once nutritive value of the food is high

enough to overcome physical limitations of rumen and alimentary tract fill, physiological regulation maintains energy intake to match requirements.

In the nonproductive animal, e.g., a moose in winter, a further increase in food nutritive value may result in a decrease in food intake (Fig. 13). Data presented by Spalinger (1980) demonstrated that when deer were fed diets of increasing digestible energy (DE) from 1.5 to 2.2 kcal/g, voluntary food intake increased. Once DE content increased from 2.2 to 3.0 kcal/g a decrease in voluntary intake was noted and MEI was constant. This suggests that intake of diets with a digestibility of 50% or less are regulated by gut capacity, while intake for diets over 50% digestible are regulated by physiological constraints (Robbins 1983).

Baumgardt (1970) has also demonstrated this principle with domestic sheep as Conrad et al. (1964) have with cattle. Furthermore, this system of physical/physiological control of food intake can be responsive to energy demands (or a lack of demand) based on the animal's production state. The relationship between voluntary DE intake and production level of an animal has been investigated by Baumgardt (1970) with domestic sheep, steers, dairy cattle, and rats. These studies indicated that as production requirements increased (i.e., maintenance vs. lactation) voluntary intake of DE/kg BW^{0.75}/d increased 2 to 3 times

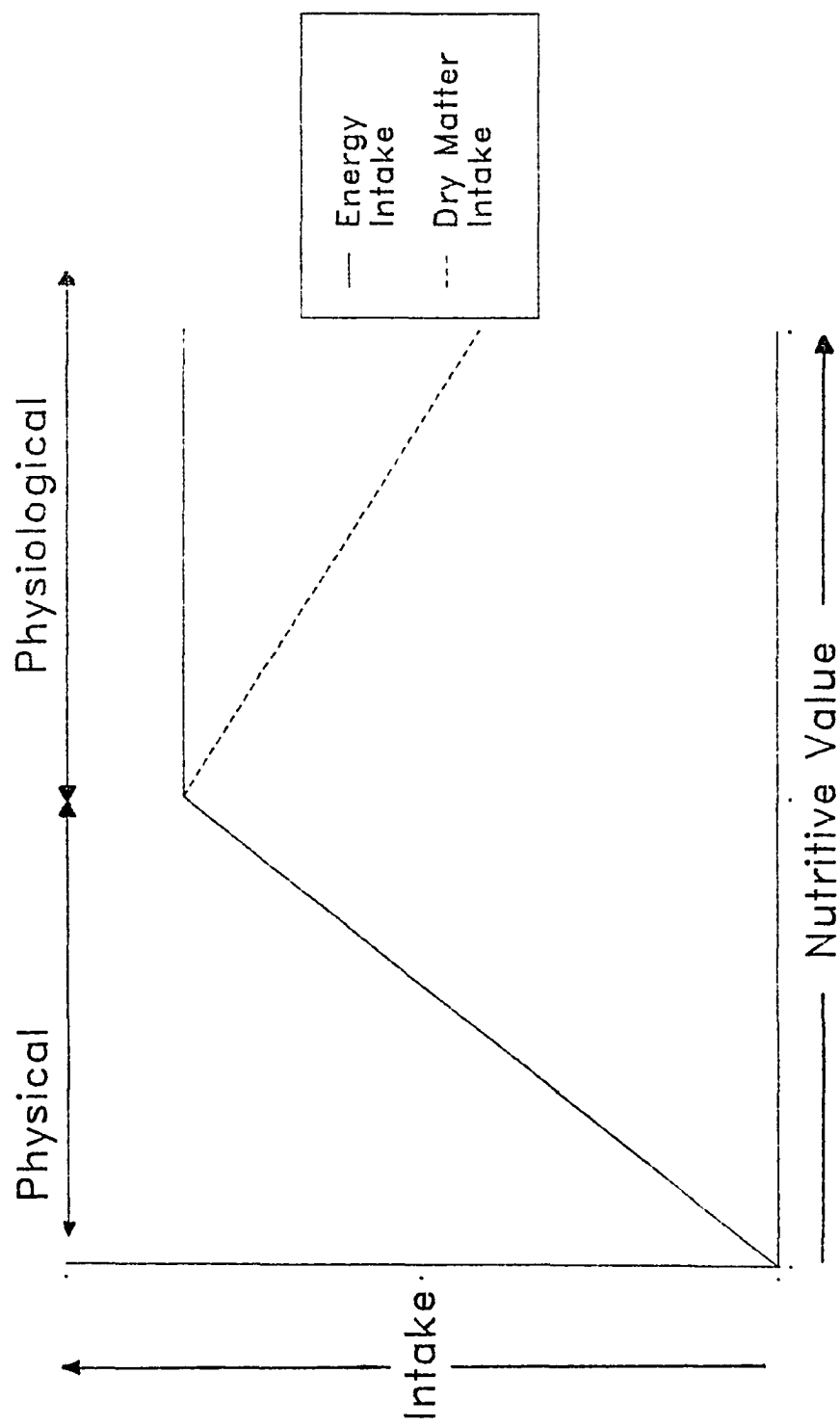


Fig. 13. Conceptual diagram of energy intake and dry matter intake in relation to increasing intake and nutritive value.

when not limited by gut fill. Likewise, studies by Montgomery and Baumgardt (1965) demonstrated that DE intake decreased as production requirements decreased during the latter stages of lactation.

Seasonal Intake

Seasonal food intake in northern cervids has been associated with reduced diet quality and forage availability during winter (LeResche and Davis 1973, Gasaway and Coady 1975). However, an endogenous rhythm that pre-adapts northern temperate cervids to the food resource can also be inferred from the numerous studies on several cervid species (McEwan and Whitehead 1970, Ozoga and Verme 1970, Westra and Hudson 1981, Wheaton and Brown 1983, Schwartz et al. 1984). These studies demonstrate a seasonal reduction in voluntary food intake accompanied by a subsequent body weight loss or stasis, when animals are offered a high quality diet ad libitum throughout the year.

Seasonal Weight Change

Production levels of the northern cervids change throughout the year in tune with production demands. Anabolism and catabolism of body energy reserves serve to adjust energy requirements to availability of food energy. Thus, seasonal variations in the body fat reserves peak at

variable times of the year between fall and spring depending on species and geographical location (Riney 1955, Flook 1970, Anderson et al. 1972).

Body fat reserves for female moose peak in late fall (25-30%) and reach a low in late spring (8-10%) (Schwartz et al. 1986b). This change in body condition appears to be linked to a voluntary annual cycle of high and low metabolic rates (Regelin et al. 1985) and seasonal food intake (Schwartz et al. 1984). Moreover, these seasonal changes in body condition appear to be independent of seasonal changes in diet quality and availability (Schwartz et al. 1986b). Furthermore, the voluntary changes in seasonal food intake appear to be correlated to animal condition (i.e., % body fat). Arnold (1985) supported this hypothesis by stating that intake decreases with increasing body fat.

Body Condition:Food Intake Relationships

The simulation model presented uses both physical and physiological control mechanisms to estimate food intake. Target body condition values (BCV) are entered as inputs to the model. Estimates of seasonal BCV for moose were obtained from controlled feeding experiments in which animals were fed a high-quality pelleted diet ad libitum throughout the year and body composition (i.e., % body fat) was estimated using tritiated water (Schwartz et al. 1986b).

The model then estimates the daily caloric and dry matter intakes required to maintain or attain BCV. This energy requirement was compared with the maximum food intake which is regulated by diet quality and maximum alimentary fill. Food intake was increased or decreased to attain the target BCV, if intake was not greater than maximum alimentary fill. Maximum alimentary fill was established as a constant related to the maximum body weight achieved. Alimentary fill was allowed to change seasonally, providing intake flexibility intake as forage availability and quality change.

The response curve between voluntary food intake and digestibility presented by Spalinger (1980) (Fig. 13) was expanded to include changes in seasonal energy demands dictated by animal production requirements (Fig. 14). Line A represents the maximum intake for any array of forage with varying digestibility (nutritive value). It simply implies that as forage quality increases, intake per unit time can also increase. At points B and C control of intake by physical limitation (i.e., gut fill) changes to physiological requirement as in Fig. 13. Point C represents the maximum intake required to meet summer demands for tissue growth and fat anabolism. Intake at point B is below the maintenance requirement for the animal and represents the period when weight loss and fat catabolism occurs (i.e.,

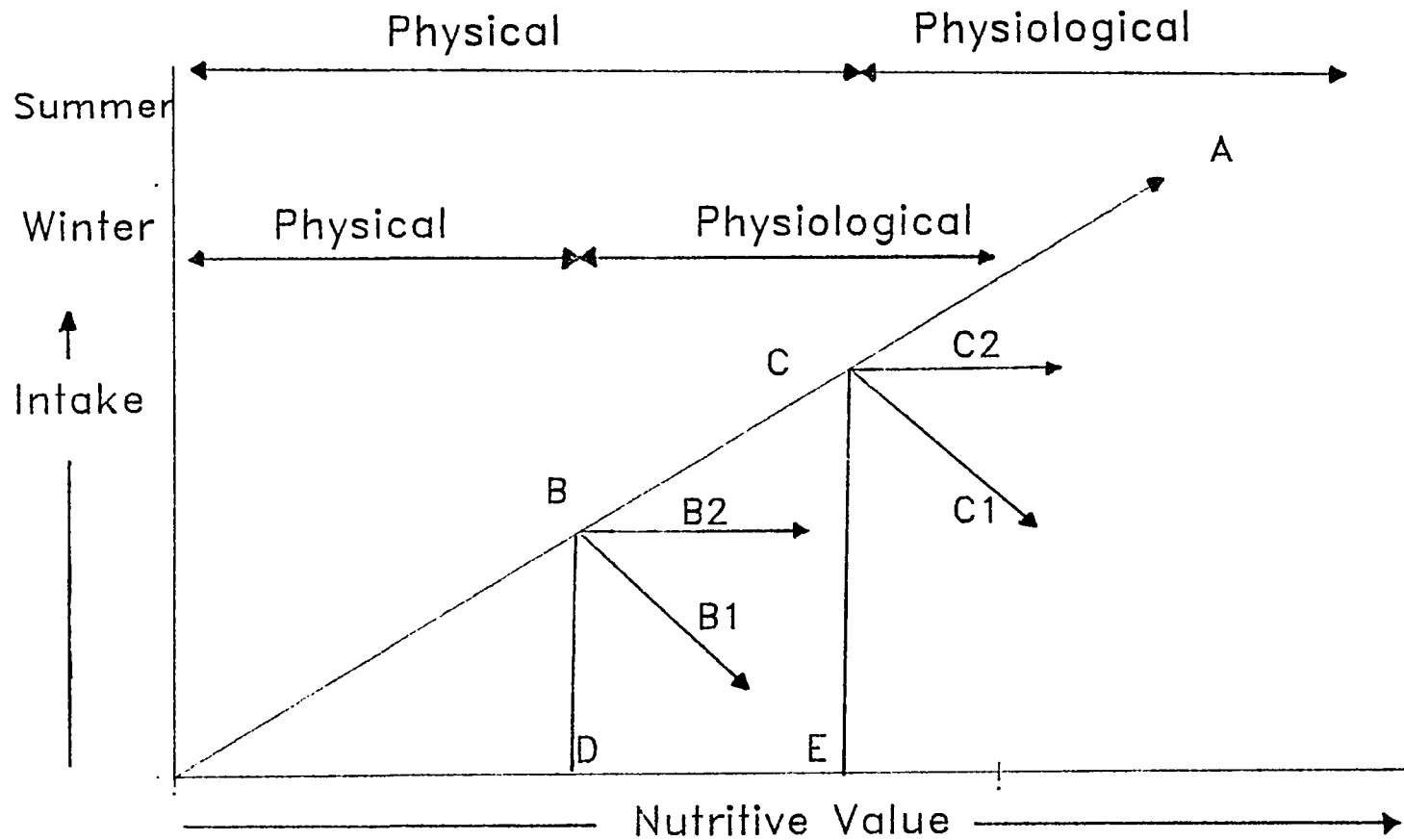


Fig. 14. Proposed seasonal relationship between energy intake and dry matter intake; A = Maximum rumen fill; B = Maximum winter caloric intake; B1 = Reduced winter intake due to diet quality; B2 = Maximum winter caloric intake; C = Maximum summer caloric intake; C1 = Reduced summer intake due to diet quality; C2 = Maximum summer energy intake; D = Minimum winter forage quality to eat to caloric intake; E = Minimum summer forage quality to eat to caloric intake.

winter). Lines B_1 and C_1 represent the physiological control mechanism that reduces intake as diet quality improves.

For moose, the line B_1 is derived from the studies by Schwartz et al. (1984) and Renecker and Hudson (1985) in which food intake was reduced in late winter even though forage quality and availability were similar to that consumed in early winter. Hence, in the present model food intake is not always determined from maximum rumen fill and this is an important deviation from that proposed by Swift (1983).

Points D and E represent minimum levels in diet quality necessary to meet winter and summer production requirements, respectively. Below these values intake is regulated by diet quality and gut fill rather than production demands. The gradient along line A between points B and C represents the dynamic status of energy requirements and the subsequent control of intake; it explains the logic behind body condition control over appetite.

Model Description

The model predicted food intake is regulated by seasonal energy demands of the animal to achieve target body conditions. This approach differs from that previously proposed by Swift (1983). In Swift's model, food intake is

regulated by rumen fill alone and body condition is the output rather than the driving variable of the model. The assumption made by Swift that ruminants always eat to rumen fill was probably incorrect (Schwartz et al. 1986b).

METHODS

Basic energy flows presented in this one-day step model are simple and only address energy partitioning (Fig. 15); the model does not deal with nitrogen balance. The model was divided into the following sections for both calculation and discussion: (1) energy costs of digestion, (2) activity energy costs, (3) summing energy costs, (4) body condition, and (5) regulation of intake. Table 16 presents a description of the variables used in the model.

Energy Costs of Digestion

Resting Metabolism:

Resting metabolism (RM) was estimated in the model and is the sum of basal metabolic rate (BMR) and heat increment (HI) of the feed. This relationship is similar to one discussed by Marston (1948) with domestic sheep. RM was estimated based on the previous 28-day metabolizable energy intake (MEIBW) ($\text{kcal/kg BW}^{0.75}/\text{d}$).

$$\text{RM} = 68.8 + (0.289 * \text{MEIBW}) \quad (1)$$

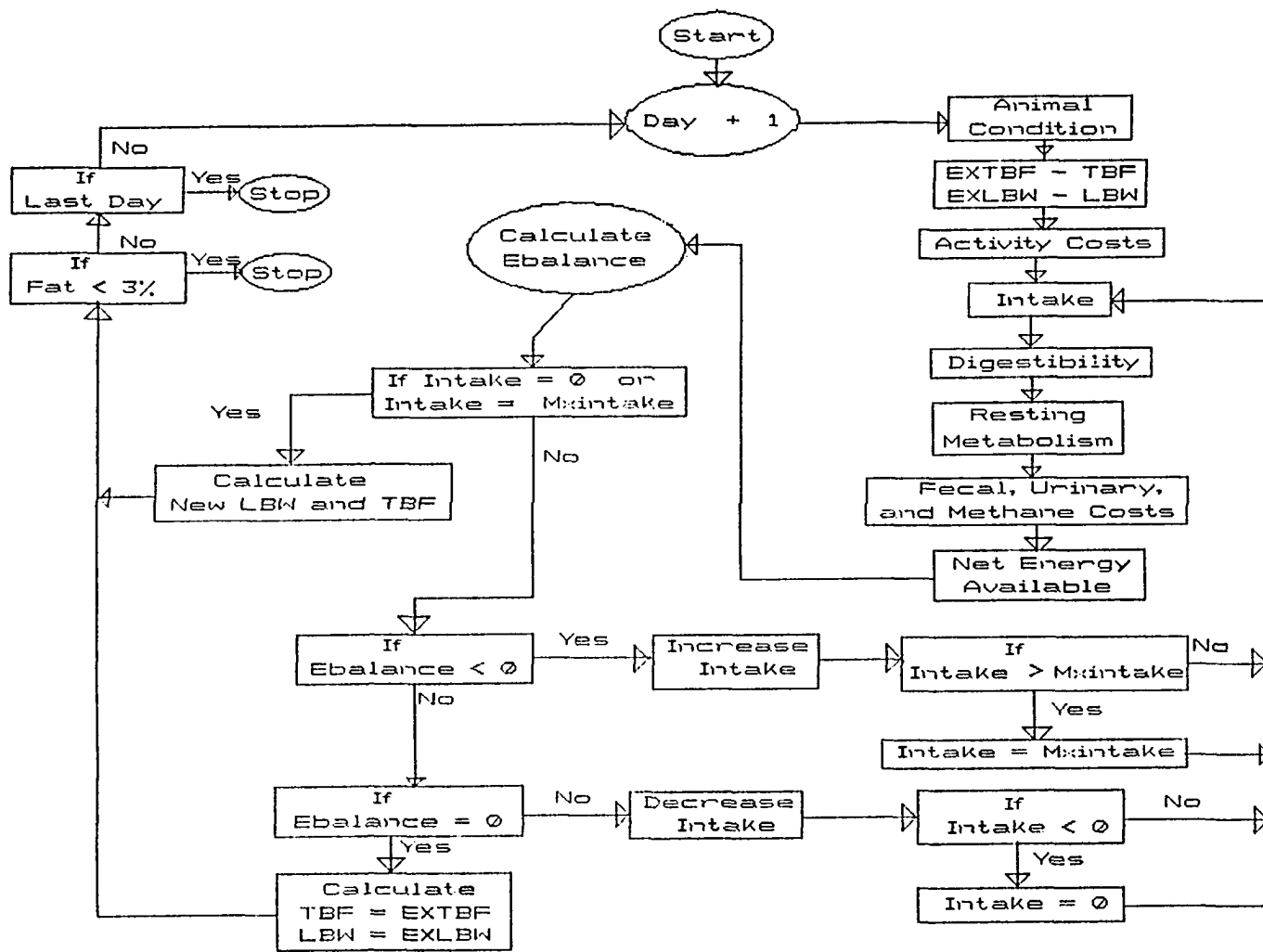


Fig. 15. Flow chart of moose simulation model. See Table 16 for description of the variables.

Table 16. Description and units of variables and constants used in the model. All rates have the implied time dimension of 1 day.

Name	Description	Units
ACTKCAL	Sum of the activity costs	kcal
AGEDAYS	Current age in days	days
BCEP	Energy pool available in BCEPL plus BCEPF	kcal
BCEPF	Energy pool available in fat	kcal
BCEPL	Energy pool available in LBW	kcal
BCV	Body condition value (TBW/TBF)	units
DIFFKCAL	Sum of DIFFTBF plus DIFFLBW converted to	kcal
DIFFLBW	Difference between EXLBW and LBW	kg
DIFFTBF	Difference between EXTBF and TBF	kg
DIG	Digestibility of the diet (g out/g in)	units
DINTAKE	Digestible energy intake	kcal
EBALANCE	The daily surplus or deficit of energy	kcal
EXLBW	Expected lean body weight from Brody curve	kg
EXTBF	Expected total body fat	%
FECAL	Fecal energy loss	kcal
FEEDING	Percentage of the day spent feeding	%
GUN	Urinary nitrogen	g
INTAKE	Intake of dry matter	g
INTKCAL	Gross energy available from intake	kcal
KCALSG	Gross energy content of the diet	kcal
KFEEDING	Energy cost for the time spent feeding	kcal
KLYING	Energy cost for the time spent lying	kcal
KSTANDING	Energy cost for the time spent standing	kcal
KWALKING	Energy cost for the time spent walking	kcal
LBW	Current lean body weight (weight-fat)	kg
LYING	Percentage of the day spent lying	%
MAINT	Energy requirements for maintenance	kcal
MAXAGE	Animal life span	days
MEIBW	Metabolizable energy intake kg BW ^{0.75}	kcal
METHANEE	Methane energy loss	kcal
MTBW	Maximum body weight ever obtained	kg
MXINTAKE	Maximum digestive tract capacity	g
MXLBW	Maximum lean body weight from Brody curve	kg
MXVN	Maximum rumen volume of nondigestibles	g
NETE	Net energy available from intake	kcal
NITRO	Nitrogen content of the diet	mg/g
STANDING	Percentage of the day spent standing	%
TBF	Current total body fat	kg
TBW	Total body weight of the animal	kg
THP	Resting metabolism	kcal
TMRT	Total mean retention time	hrs
URINEE	Urinary energy loss	kcal
WALKING	Percentage of the day spent walking	%
XKCAL	Surplus energy available	kcal

Fecal Energy Loss:

Daily fecal energy loss (FECALE, kcal) is inversely related to the digestibility of the diet (DIG) and is calculated as follows:

$$\text{FECALE} = \text{INTAKE} * (1 - \text{DIG}) * \text{KCALSG} \quad (2)$$

where INTAKE is daily dry matter intake (g) and KCALSG is the average caloric content (usually 4.5 kcal/g) (Golley 1961, Milchunas et al. 1978) of the diet.

Urine Energy Loss:

Because a major portion of the energy lost in urine comes from protein metabolism, daily urinary energy loss (URINEE, kcal) was related to nitrogen content (NITRO, g/100g) of the diet and to intake. Equations 3 and 4 calculate daily urinary nitrogen (GUN, g) which was converted to caloric loss from data derived for moose and reported by Schwartz et al. (1986c).

$$\text{GUN} = ((.5607 * (\text{NITRO} * \text{INTAKE}) * \text{TBW}^{0.75}) + .05607) / \text{TBW}^{0.75} \quad (3)$$

$$\text{URINEE} = 307.3 + (8.327 * \text{GUN}) \quad (4)$$

Methane Energy Loss:

Methane is a by-product of microbial fermentation in the rumen and lost through eructation. Estimation of daily methane energy loss (METHANEE, kcal) was derived from an equation presented by Swift (1983) using data from cattle and sheep (Blaxter and Clapperton 1965).

$$\text{METHANEE} = 3.64 + (7.5 * \text{DIG}) + (\text{DINTAKE} / \text{MAINT}) * (1.03 - (2.8 * \text{DIG}))$$

(5)

DINTAKE is daily digestible energy intake (kcal), and MAINT is daily maintenance energy requirement (kcal).

Activity Energy Costs

Energy expenditure associated with various activity for moose has been estimated by Renecker and Hudson (1983) using a calibrated heart rate index. Inputs are based on percentage of a day spent at each activity.

Cost of Lying:

The cost of lying is the mean cost from 3 different lying or bedded activities, dozing, alert, and ruminating (Renecker and Hudson 1983):

$$\text{KLYING} = ((\text{LYING}/100) * (0.1433 * 24)) * \text{TBW}^{0.75} \quad (6)$$

where KLYING is the daily energy cost for time spent lying (kcal), 0.1433 is a constant which estimates caloric cost per h/kg BW^{0.75}, and 24 is a constant converting a day to hours.

Cost of Standing:

$$\text{KSTANDING} = ((\text{STANDING}/100) * (0.8122 * 24)) * \text{TBW}^{0.75} \quad (7)$$

KSTANDING is the daily energy cost for time spent standing (kcal), STAND is the percent of day spent standing, 0.8122 is a constant which estimates caloric cost per h/kg BW^{0.75} to stand, and 24 is a constant to convert day to hours (Renecker and Hudson 1983).

Cost of Feeding:

Feeding cost was estimated by Renecker and Hudson (1983) from moose feeding at 4 different height planes: cratering at ground level and feeding on vegetation at 3 different heights (low, middle, high). The mean value for all these activities was used in the model. The equation to calculate costs of feeding was:

$$KFEEDING = ((FEEDING/100) * (1.0332 * 24)) * TBW^{0.75} \quad (8)$$

where KFEEDING is the daily cost for time spent feeding (kcal), FEEDING is percent of the day spent feeding, 1.0322 is a constant for cost (kcal) per h/kg BW^{0.75} to feed, and 24 is a constant to convert day to hours.

Cost of Walking:

The cost of walking represents only the time spent walking; no adjustments for speed or slope were made.

$$KWALKING = ((WALKING/1000) * (1.8872 * 24)) * TBW^{0.75} \quad (9)$$

where KWALKING is the daily cost for time spent walking (kcal), WALK is percent of the day spent walking, 1.8872 is a constant for the cost (kcal) per h/kg BW^{0.75} to walk, 24 is a constant to convert day to hours (Renecker and Hudson 1983).

Summing of Activity Costs:

$$ACTKCAL = KLYING + KSTANDING + KFEEDING + KWALKING \quad (10)$$

ACTKCAL is the daily energy cost of activities.

Summing of Energy Costs

Energy retained for production (NETE, kcal/d) is calculated as energy inputs minus energy losses. Intake of dry matter is converted to calories by multiplying intake by the kcals of gross energy in the forage. This value represents energy input (INTKCAL). Energy losses are then subtracted from INTKCAL. These energy losses represent fecal, urine, methane, resting metabolism, and activity costs. The equation to calculate net energy was:

$$\text{NETE} = \text{INTKCAL} - (\text{FECALE} + \text{URINEE} + \text{METHANEE} + \text{RM} + \text{ACTKCAL}) \quad (11)$$

where NETE is net energy available before depleting or building body reserves, INTKCAL is kcals gross energy in INTAKE.

Body Condition

Body condition is the critical driver of the model. All estimates of intake relate to BCV (body condition value, TBF/TBW) with maximum intake controlled by maximum alimentary fill. However, if the animal is not required to eat to maximum rumen fill to meet the energy demands, then intake is regulated by BCV (i.e., physiological control).

Estimated Lean Body Weight:

The expected lean body weight (EXLBW, kg) in relation to age was calculated from a Brody curve (Brody 1945) adjusted for moose. The adjustments were made to the shape parameter using data presented by Schwartz et al. (1984, 1986d) resulting in the following equation:

$$\text{EXLBW} = \text{MXLBW} * (1 - e^{(-9.1 * \text{agedays}) / \text{MXAGE}}) \quad (12)$$

where MXLBW is maximum lean body weight (kg), -9.1 is a shape parameter for the curve, AGEDAYS is the current age in days, and MXDAYS is maximum life span for a moose.

Expected Total Body Fat:

Expected total body fat (EXTBF, kg) for the model is an input parameter. It was determined by controlled feeding experiments with moose offered a high quality diet ad libitum and by estimating BCV throughout the year. BCV represents the current physical body condition of a moose given by its fat reserves.

Weight Loss:

Under the constraints of this model, body condition dictates intake. Thus, if the animal has more fat than required to meet the expected BCV, it must burn its fat

stores and loses weight. This is accomplished by reducing intake, thereby putting the animal in negative energy balance. The model assumes 100% efficiency of energy utilization from body stores. Weight loss occurs as follows: if the animal's EXTBF is less than TBF the difference is added to a bookkeeping value (BCEPF, kcal) within the model.

$$\text{DIFFTBF} = \text{TBF} - \text{EXTBF} \quad (13)$$

$$\text{BCEPF} = \text{DIFFTBF} * 9.4 * 1000 \quad (14)$$

DIFFTBF (kg) is the difference between total body fat and expected total body fat. Body fat has a caloric value of 9.4 (Torbit 1981), and 1000 converts g to kg.

Torbit (1981) reported that when fat catabolism occurred, loss of LBW also occurred. In mule deer (Odocoileus hemionus) for each kg of fat lost there was a corresponding 0.43 kg loss of LBW. This is accounted for in the model by reducing LBW proportionally with TBF loss. Energy available for metabolism from each unit LBW loss is calculated as described by Swift (1983) where:

$$\text{DIFFLBW} = \text{DIFFTBF} * 0.43 \quad (15)$$

$$\text{BCEPL} = ((0.3056 * (\text{DIFFLBW} * 1000)) + (0.6944 * 0.449 * (\text{DIFFLBW} * 1000))) / 0.29$$

where DIFFLBW (kg) loss of LBW, 0.43 is the proportion of LBW loss related to TBF (Torbit 1981), BCEPL (kcal) is a variable used for summation purposes, 0.3056 is non-nitrogenous energy per unit LBW, 0.6944 is nitrogenous energy per unit LBW, 0.449 is a constant for the efficiency of the deanimation process, 1000 converts kg to g, and 0.29 converts to a dry matter basis (van Es 1977).

BCEPF and BCEPL are summed to a variable (BCEP) which is used only for summation during calculations.

$$\text{BCEP} = \text{BCEPF} + \text{BCEPL} \quad (16)$$

Weight Gain:

When current body weight is less than expected body weight, the model attempts to make the simulated animal gain weight. Weight gain can be achieved in 3 ways:

1) Lean Body Weight Gain

When EXTBW equals TBF and LBW is less than EXLBW then deposition of LBW takes place, when energy is available. In this case, food intake increases to meet energy required to obtain EXLBW with the following:

$$\text{DIFFLBW} = (\text{LBW} - \text{EXLBW}) * (5.4 * 1000 * 0.71) \quad (17)$$

where 5.4 is the caloric value of LBW, 1000 converts kcal/g to kcal/kg, and 0.71 increases the energy required to meet energy demands for deposition of LBW since the process is only 71% efficient.

2) Gain Fat

If LBW is equal to EXLBW, but TBF is less than EXTBF, the animal will store fat when surplus dietary energy is available.

$$\text{TBF} = \text{TBF} + (\text{XKCALS} / (9.4 * 1000 * (0.71))) \quad (18)$$

XKCALS (kcal) is the surplus energy available from dietary metabolizable energy, 9.4 is the energy content of fat (kcal/g), 1000 converts g to kg, and this process is assumed 71% efficient (0.71).

3) Gaining Fat Plus Lean

If both TBF and LBW are below expected values (i.e., EXTBF and EXLBW) the animal will gain lean body weight and store fat in the ratio given by Torbit (1981).

$$\text{DIFFLBW} = (\text{LBW} - \text{EXLBW}) * (5.4 * 1000 * 0.71) \quad (19)$$

$$\text{DIFFTBF} = (\text{TBF} - \text{EXTBF}) * (9.4 * 1000 * 0.71) \quad (20)$$

$$\text{DIFFKCAL} = \text{DIFFLBW} + \text{DIFFTBF} \quad (21)$$

If DIFFKCAL cannot be achieved with energy available from food intake (kcal) then energy is partitioned to LBW and TBF as follows:

$$\text{LBW} = (((\text{XKCAL} * .7) / (5.4 * 1000 * 0.71))) / 1000 \quad (22)$$

$$\text{TBF} = (((\text{XKCAL} * .3) / (9.4 * 1000 * 0.71))) / 1000 \quad (23)$$

Regulation Of Food Intake

Food intake was estimated in a multi-step process in which the predicted intake required to meet target BCV was compared with the maximum intake possible (MXINTAKE, g) for the current diet digestibility. Determination of INTAKE and INTKCAL was described above, and MXINTAKE was determined based on the results from maximum intake levels recorded from moose (Schwartz et al. 1984, 1986b). MXINTAKE is a function of TMRT and maximum nondigestible alimentary fill (MXVN, g).

The steps are as follows:

1) calculate TMRT (h) for the current intake

$$\text{TMRT} = 60.860 - (0.2366 * (\text{INTAKE} / \text{MTBW})^{0.75}) \quad (24)$$

2) calculate the maximum alimentary fill (MXVN, g/24 h)

$$\text{MXVN} = (130\text{g} / \text{MTBW}) * ((1 - 0.56 / 24) * \text{TMRT}) \quad (25)$$

3) calculate the maximum intake (MXINTAKE, g/24 h)

$$\text{MXINTAKE} = \text{MXVN} + (\text{MXVN} * \text{DIG}) / (2 * (1 - \text{DIG})) \quad (26)$$

If INTAKE < MXINTAKE -----> use INTAKE

If INTAKE > MXINTAKE -----< use MXINTAKE

DIG is the digestibility of the diet, 0.56 is a constant (Schwartz et al. 1986b) and MTBW (kg) is the maximum total body weight ever attained by the animal.

Energy Balance:

Energy balance (EBALANCE, kcal/d) in the model is the energy required to achieve target BCV (i.e, EXTBF and EXLBW). Energy required to meet the target BCV is added or subtracted to the gross energy intake and energetic costs are subtracted from this total. This provides that EBALANCE is equal to 0 to meet target BCV goals. If EBALANCE is >0 the animal will reduce energy intake to meet target BCV. If EBALANCE is <0 then energy intake is increased to meet BCV

goals. However, if energy intake cannot meet BCV goals due to limits of alimentary fill, the animal will eat to maximum alimentary fill.

$$\text{EBALANCE}=\text{DIFFKCAL}+\text{NETE} \quad (27)$$

RESULTS AND DISCUSSION

Computer simulation models should be tested against empirical data. When this type of data is unavailable, model testing is reduced to uncovering program errors (Hudson and White 1985). I have been able to test the moose nutrient control model against empirical data, and from these tests can discuss theoretical implications to energy partitioning.

Model Inputs

This simulation model is based on an adult nonproductive female moose with the starting values for the model given in Table 17. Monthly inputs are used for forage qualities (nitrogen content and digestibility of the diet) (Table 18). Also, EXTBF values are entered on a monthly basis and daily interpolations are made to smooth the transition between months. Activity costs were also entered monthly; however, only data from winter activity studies

Table 17. Starting inputs for the simulation of an adult nonpregnant female moose.

Age (days)	1250
Total body weight (kg)	450
Total body fat (kg)	108
Maximum lean body weight (kg)	350
Starting day (Julian)	1
Ending day (Julian)	366

Activity (% of day)^a

Standing	4.7
Walking	3.2
Feeding	40.6
Lying	51.5

^a Fixed values are used because only 1 report of activity was available.

Table 18. Model inputs for body fat, food digestibility, and nitrogen content of the diet by Julian day. The model interpolates between input values.

Julian Day	Nitrogen (g/100g)	Digestibility (g/100g)	Body Fat (%)
1	0.0106	0.315	26
32	0.0109	0.312	24
60	0.0109	0.315	22
91	0.0112	0.333	18
121	0.0300	0.560	16
152	0.0250	0.531	18
182	0.0250	0.531	21
213	0.0250	0.447	22
244	0.0214	0.420	23
274	0.0214	0.396	23
305	0.0101	0.376	24
335	0.0106	0.315	25

were available so activity had to be treated as a constant throughout the year.

Sensitivity Analysis

Sensitivity analysis of the model was done by increasing the key parameters DIG, THP, TMRT, MXINTAKE, and ACTKCAL by 10% and monitoring change in the sum of yearly food intake (Table 19). The validation runs were started on January 1 and run through December 31.

Model sensitivity to key parameters affected the sum of yearly intake differently. DIG had the greatest effect and decreased food intake by 10.9% a year. This is less than what might be expected (White 1983); however, during the simulation runs with this model, food intake termination was not usually based on gut fill, but rather on caloric fill. Therefore, increasing digestibility 10% would decrease intake by the same amount to off-set increased caloric intake. At times when gut fill was the controlling variable, the increased digestibility would allow for increased intake. A 10% increase in THP only increased food intake 7.6%. Increasing TMRT or MXINTAKE both increased intake by 6.5%, and ACTKCAL had only a slight effect (0.9%) on yearly intake.

Initial validation runs of the model were done to establish whether the model processes were reacting as

Table 19. Model sensitivity to a 10% increase in input variables. Sensitivity observed in the change in predicted yearly food intake of a nonproductive female moose.

Variable	Description	Yearly Intake (%)
DIG	Diet digestibility	-10.9
THP	Resting metabolism	7.6
TMRT	Time in dig. tract	6.5
MXINTAKE	Maximum intake	6.5
ACTKCAL	Activity costs	0.9

proposed. A model simulation of Julian day 1-365 was done comparing seasonal inputs of DIG, TBF, and nitrogen content with corresponding seasonal outputs of the model, and no differences were noted. Fig. 16 presents the simulated seasonal fluctuation in body fat and body weight of a nonproductive female moose. Seasonal changes in diet digestibility used by the model are presented in Fig. 17, which show the dramatic increase in food digestibility in late spring and the slow decline throughout fall.

In Fig. 18 the RM estimate calculated by the model is plotted on metabolizable energy intake ($\text{kcal/kg BW}^{0.75}/28 \text{ d}$ mean). Also shown is the line produced by eq. 1 and demonstrates that the equation used in the model was reacting as designed.

TMRT was also simulated and checked against the regression equation (eq. 24); used in the model (Fig. 19). This shows the predicted line (eq. 24), and the variation around the line, which occurs with large shifts in daily body weight. This error occurs because the body weight that is used to predict TMRT is the previous day's weight and not the current day's weight which was not yet estimated. The inverse relationship between alimentary fill ($\text{g/kg BW}^{0.75}$) and TMRT is shown in Fig. 20. This shows the seasonal effects of intake on TMRT and alimentary fill which are controlled by food quality and intake.

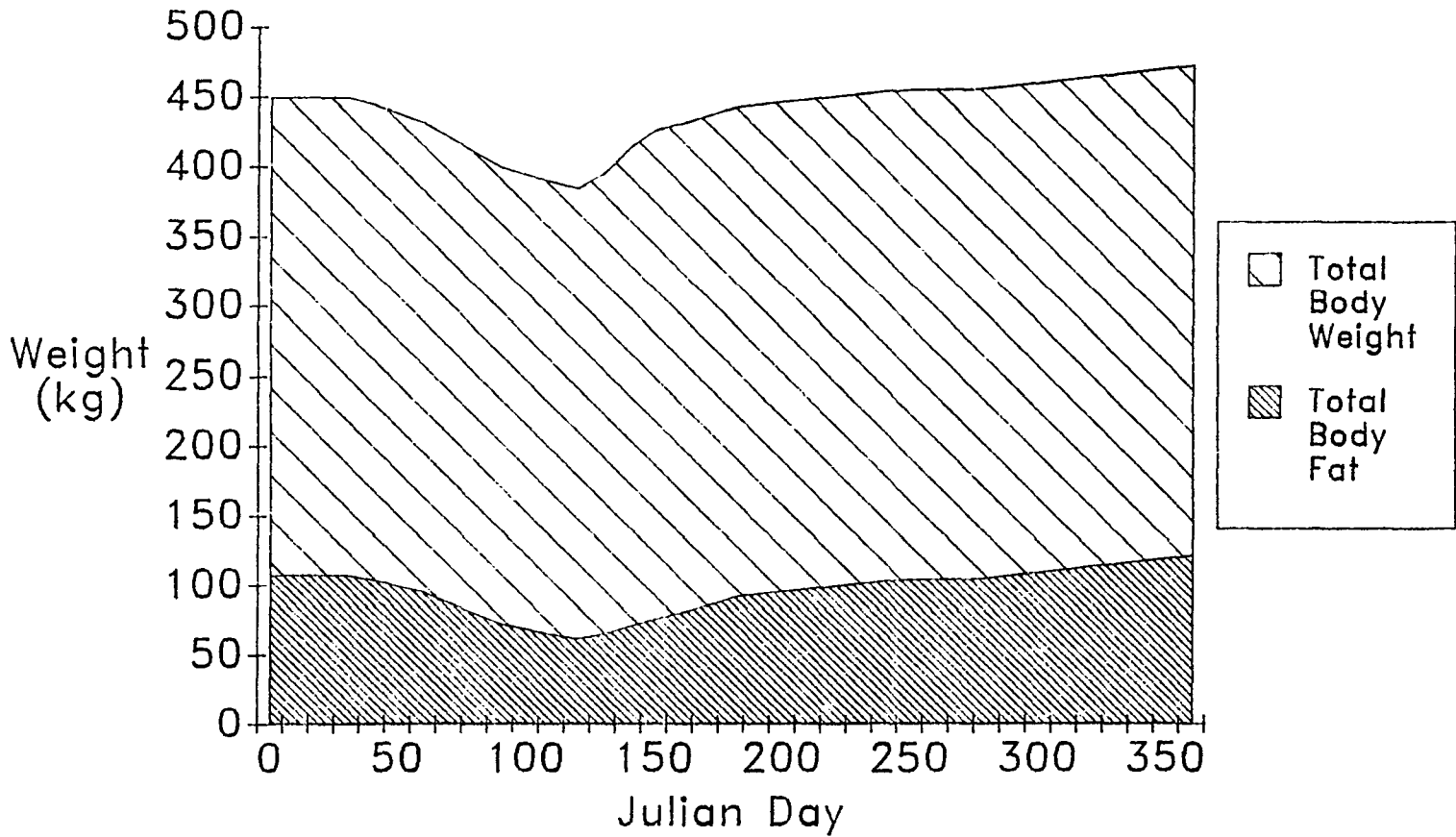


Fig. 16. Simulation model inputs of total body fat and predicted total body weights for a moose.

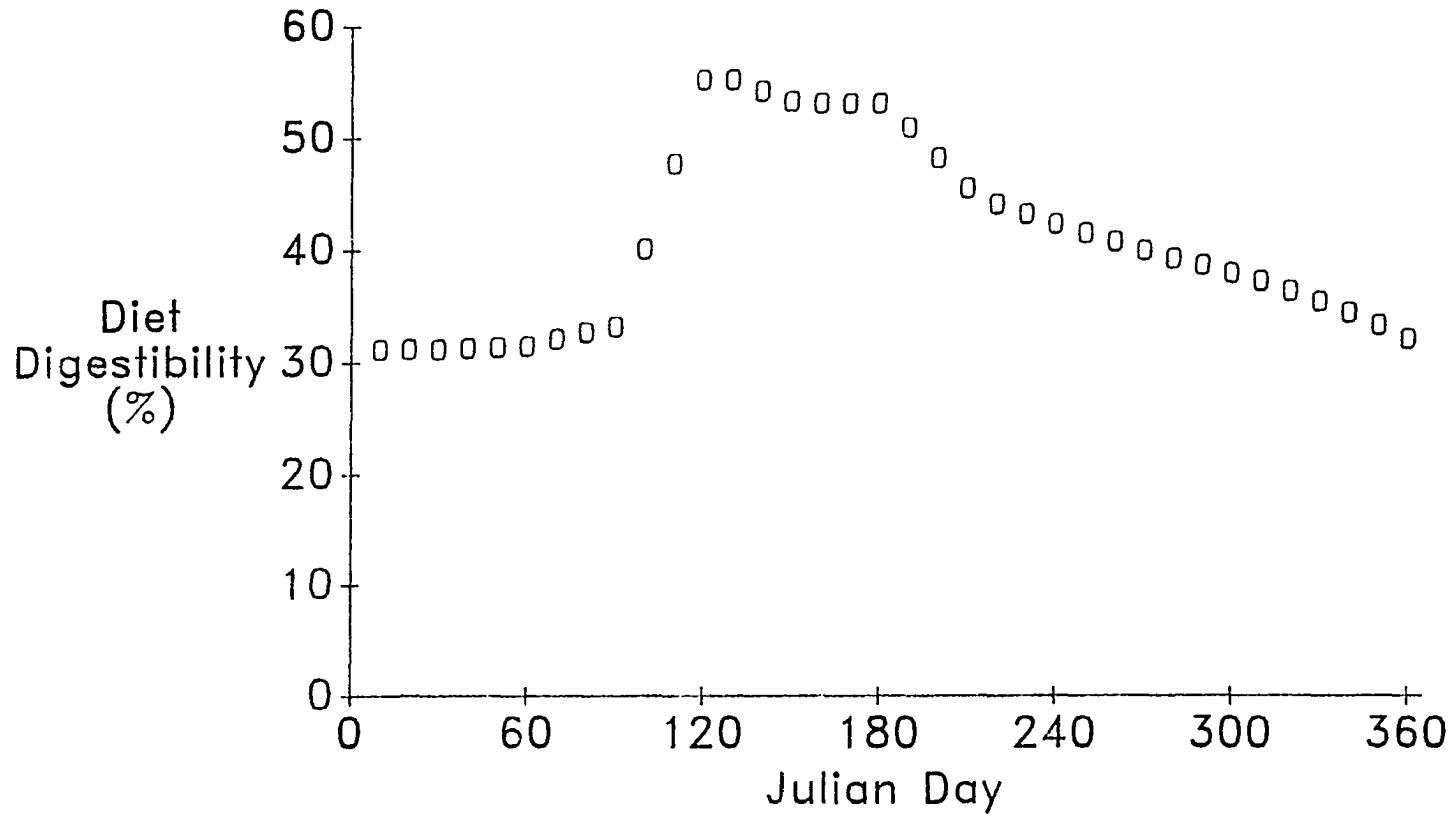


Fig. 17. Diet digestibility inputs for a moose simulation model.

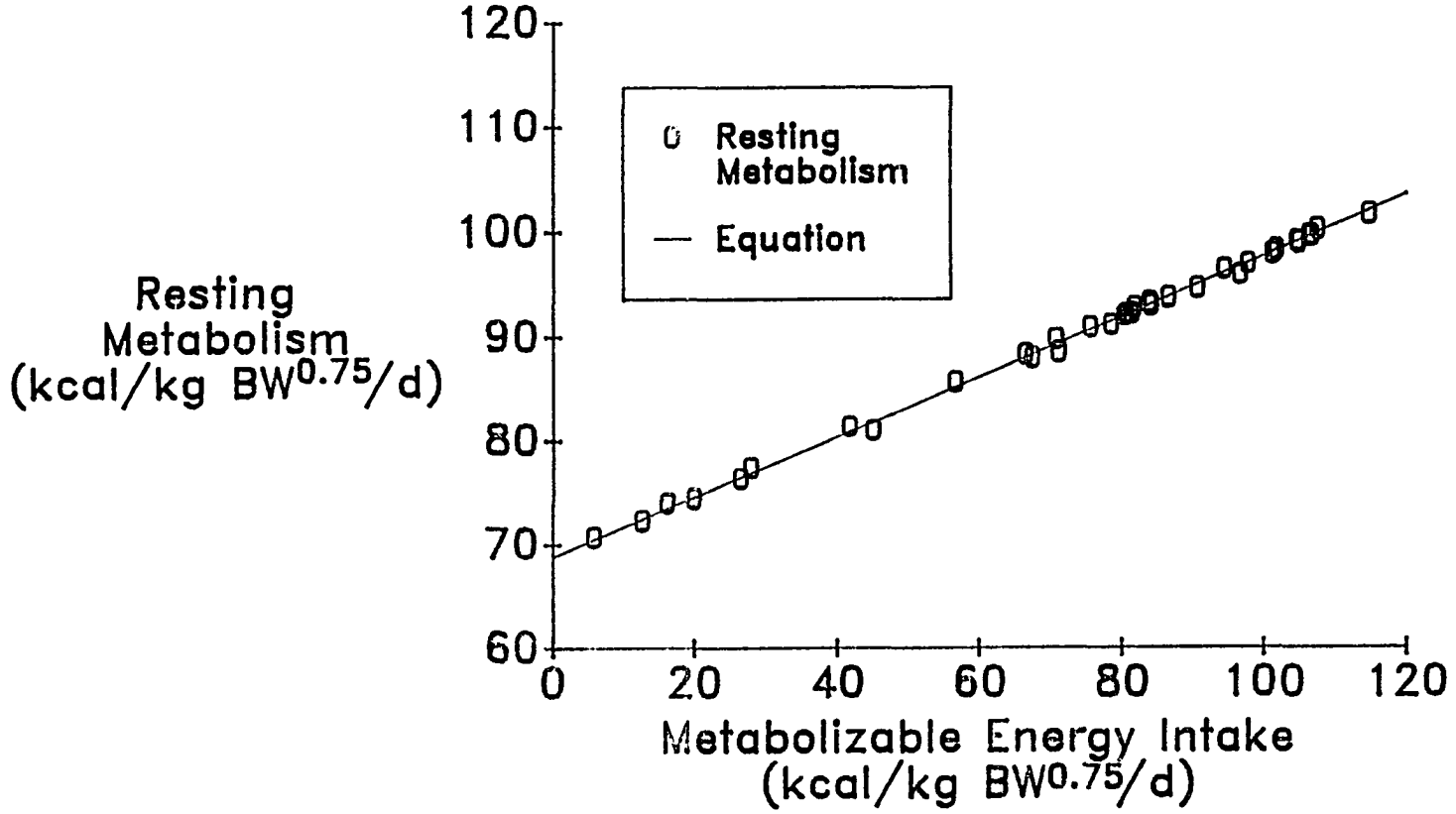


Fig. 18. Model-predicted resting metabolism (Y) and metabolizable energy intake of (X) (previous 28 d mean intake). The solid line is produced from an equation in the model ($Y=68.8+0.289X$) for resting metabolism of moose.

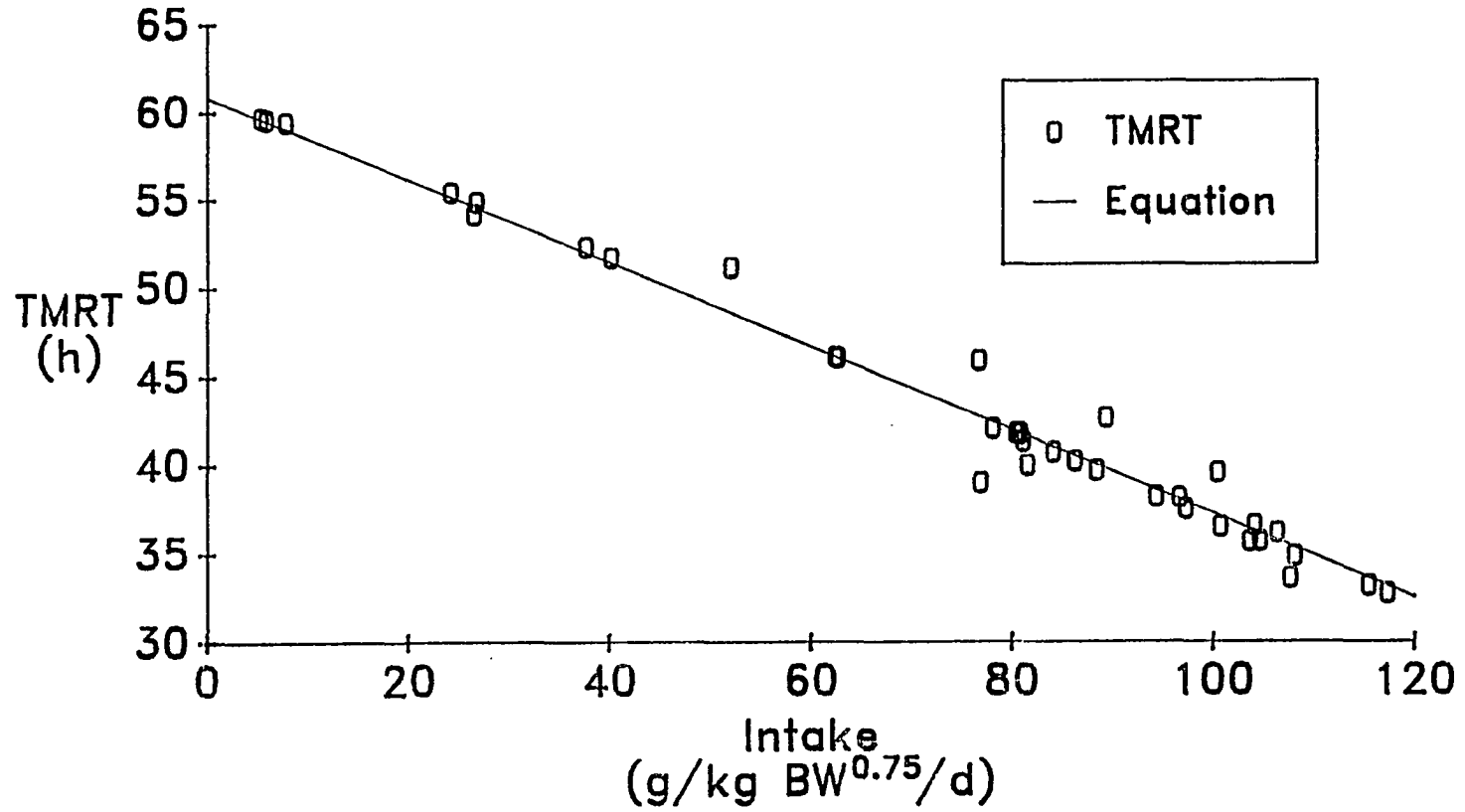


Fig. 19. Model-predicted total mean retention time of particulates (Y) (TMRT) on food intake (X) g/kg BW^{0.75}/d. The solid line is produced from an equation in the model ($Y=60.9-0.237X$) for TMRT of moose.

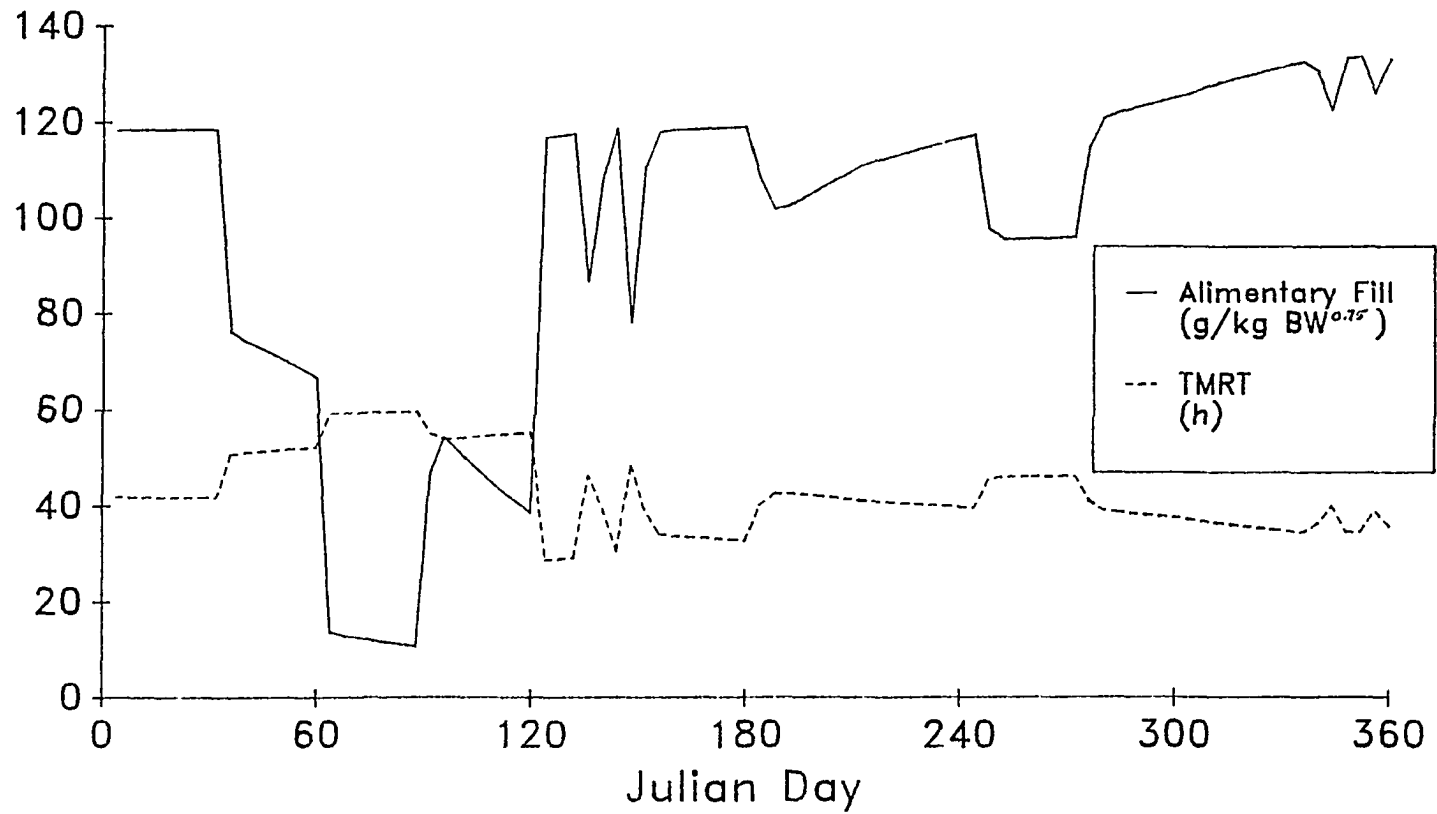


Fig. 20. Comparison of simulation model-predicted alimentary fill and particulate total mean retention time (TMRT) of moose.

Predicted Seasonal Intake

Yearly intake predicted by the model (Fig. 21) shows the same seasonal trends as those reported by Schwartz et al. (1984) and Renecker and Hudson (1985). However, the predicted intake is more erratic because only 12 inputs of DIG and EXTBF are used. Partial smoothing of the predicted intake could be accomplished if polynomial equations were used for all input variables.

Predicted Maintenance Requirements

Further testing of the model was done by comparison of predicted winter maintenance requirements with empirical data reported by Schwartz et al. (1986b). However, Schwartz and coworkers reported winter maintenance of a mixed cohort including males and productive and nonproductive females rather than just the nonproductive female as the model simulates. Model validation runs were designed to cover the same seasonal period (21 Nov-22 Apr) as the empirical study (Fig. 22). Maintenance requirement predicted by the model is 122.2 compared to 140.8 (kcal digestible energy/kg $BW^{0.75}/d$) reported by Schwartz and coworkers. This 15% difference may be due to the model's overestimation of feed energy, underestimation of energy costs, or the difference in energetic costs associated with the mixed cohort animals.

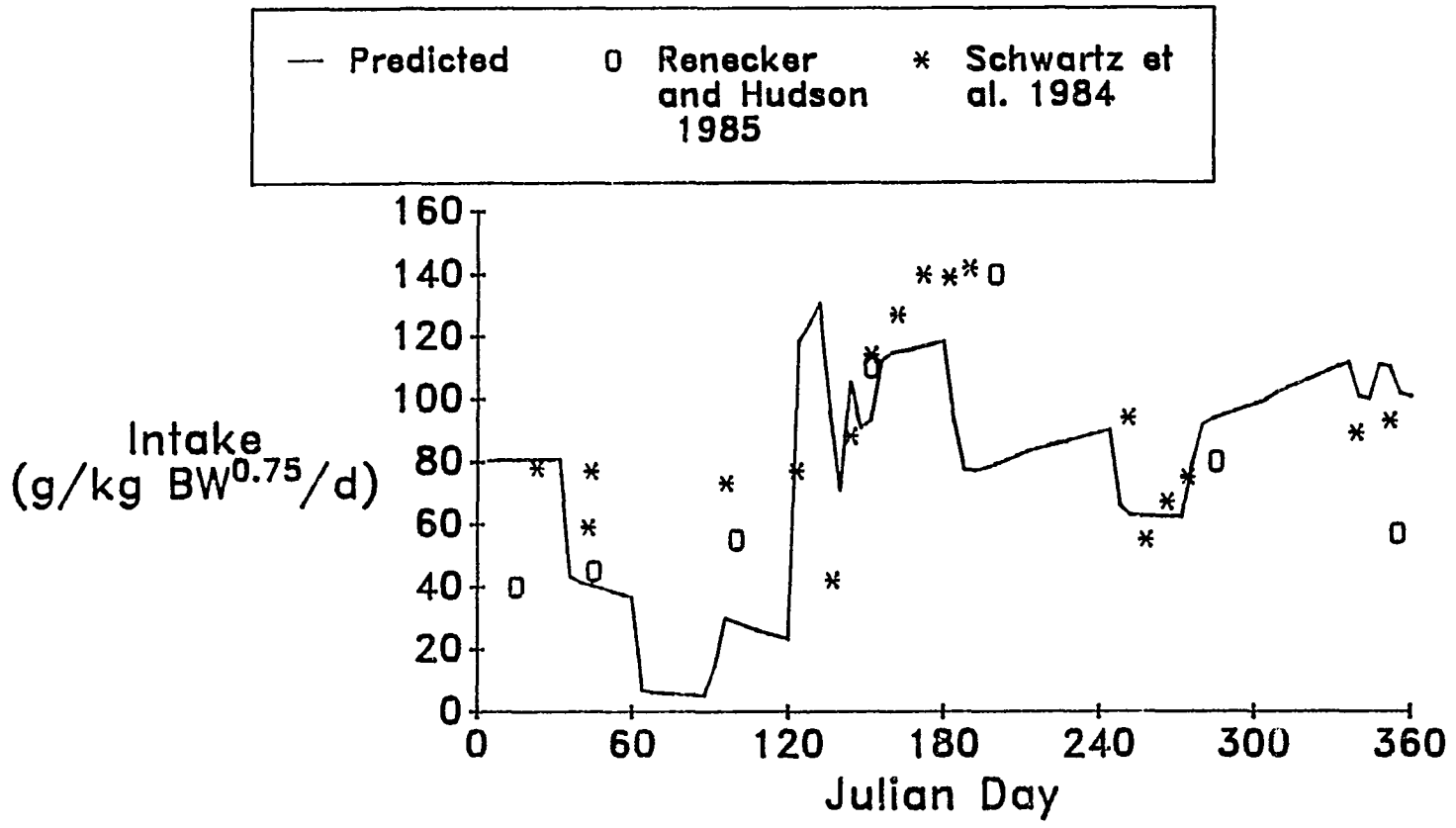


Fig. 21. Comparison of simulation model-predicted food intake with reported food intake levels for moose.

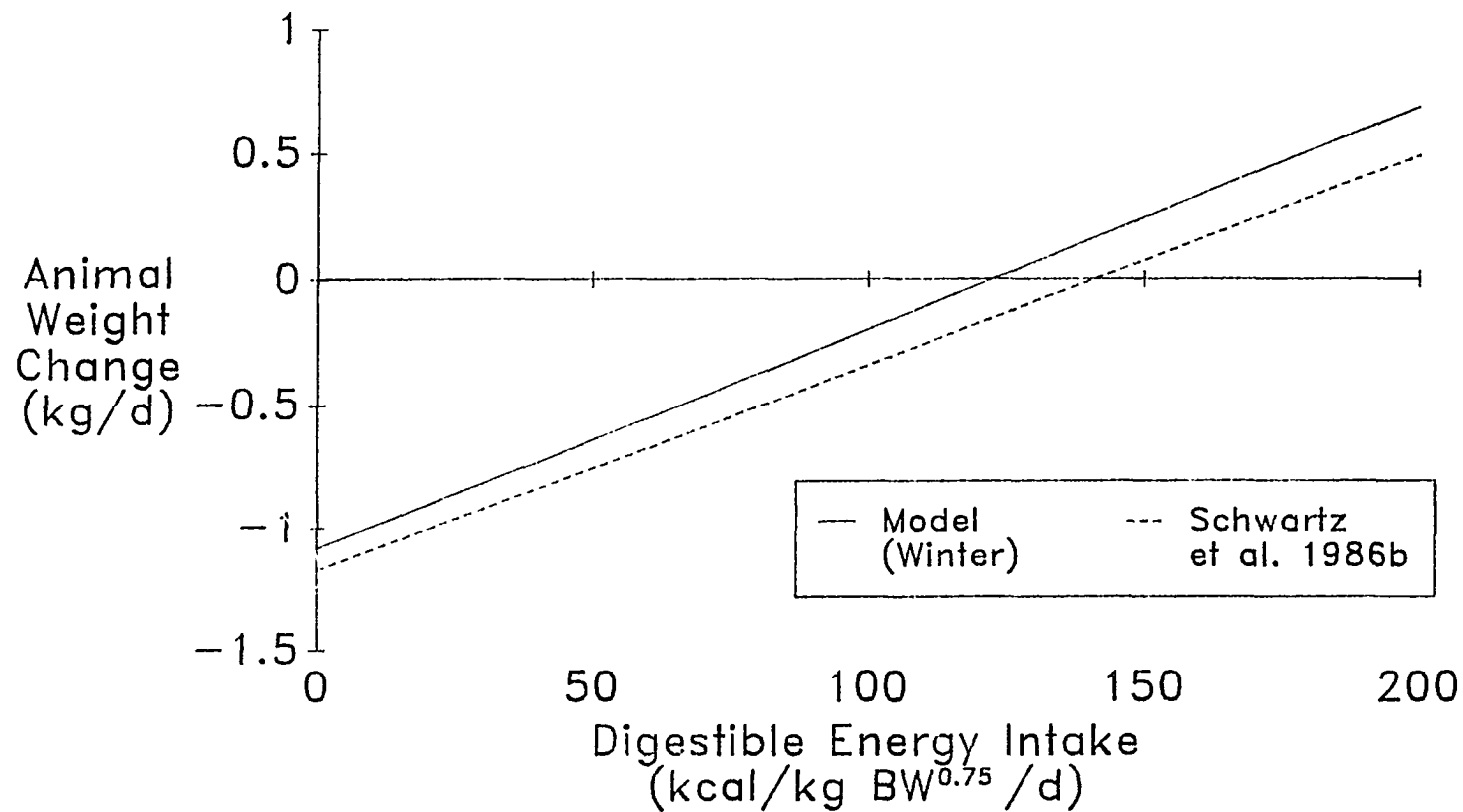


Fig. 22. Comparison of model-generated and reported digestible energy requirements for maintenance of moose.

Maintenance energy requirements are known to change seasonally (Fig. 23, Table 20) and this was tested by regressing seasonal weight change with digestible energy intake. In the model, digestible energy (DE) requirements for maintenance changed seasonally with fall (112.3) being lower than winter (122.2) or summer (120.6 kcal DE/kg $BW^{0.75}/d$).

Previous Feeding Level

To evaluate the influence of previous feeding level on energy balance, example calculations were made using the equation for RM (eq. 1).

$$RM = 68.8 + 0.289x$$

x=28 d mean metabolizable energy intake

Using RM as an estimate of heat production, energy balance was derived by subtracting RM from metabolizable energy intake (MEI) (Lofgreen and Garrett 1968).

$$\text{Energy balance} = \text{MEI} - \text{RM}$$

Fig. 24 shows the relation of energy balance with energy intake with this simulation run (solid line). However, because plane of nutrition is known to affect RM (Marston 1948), additional simulations were made to determine the energy balance:current digestible energy intake relationship when the previous digestible energy intake was high or low. The high plane of nutrition (solid line) indicates an

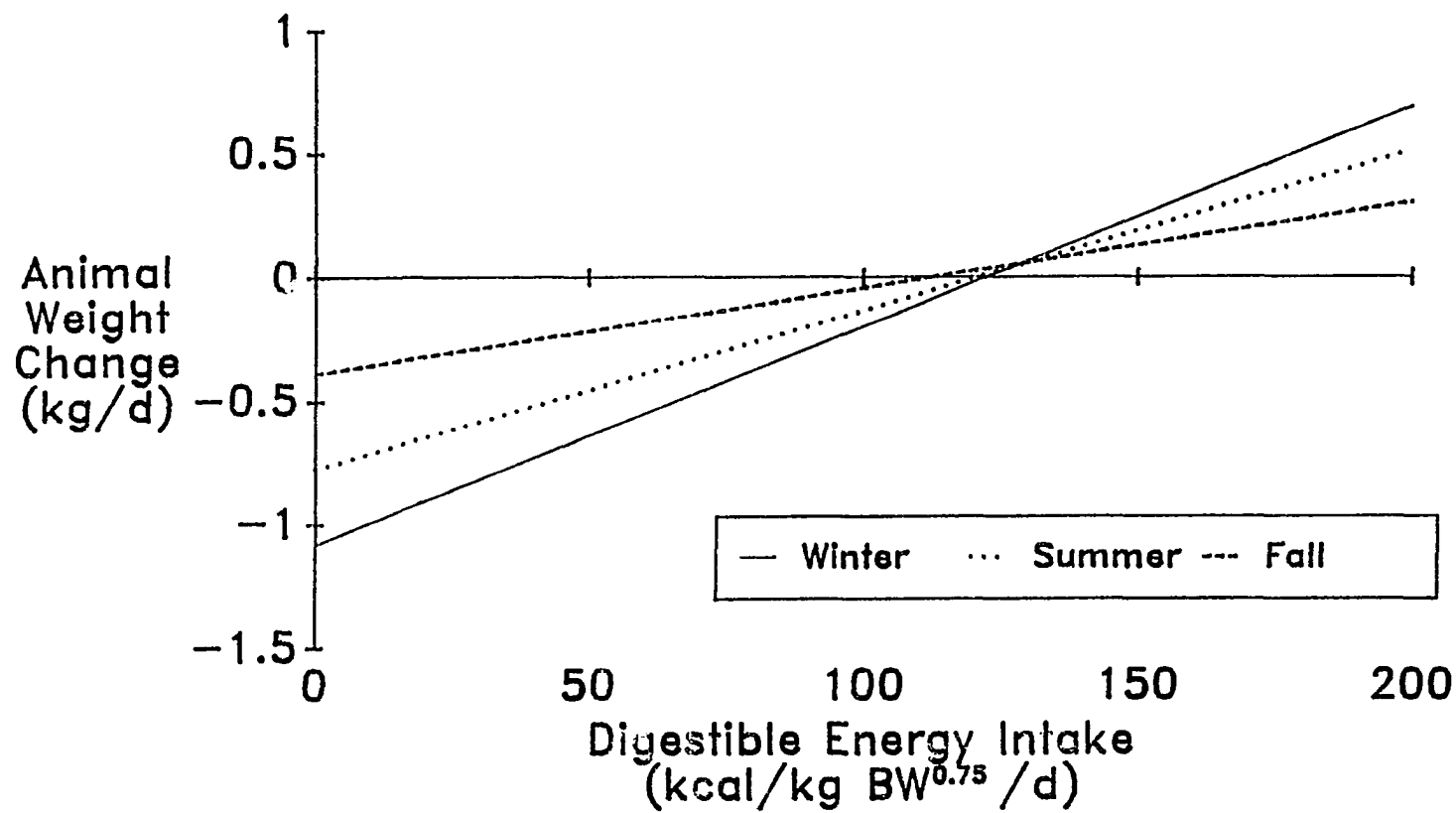


Fig. 23. Model-generated digestible energy requirements for maintenance of a nonproductive adult female moose.

Table 20. Predicted seasonal estimates of digestible energy required for maintenance of nonproductive female moose.

Julian Day	Season	$Y = a + bX$	Maintenance (kcal/ $\text{kgBW}^{0.75}/\text{d}$)
1 - 365	Year	$Y = -0.95892 + 0.00724$	132.4
335 - 101	Winter	$Y = -1.08308 + 0.00886$	122.2
102 - 218	Summer	$Y = -0.77566 + 0.00643$	120.6
219 - 334	Fall	$Y = -0.38983 + 0.00347$	112.2
Gaining weight only		$Y = -0.80760 + 0.00641$	126.0
Losing weight only		$Y = -1.15477 + 0.01055$	109.5

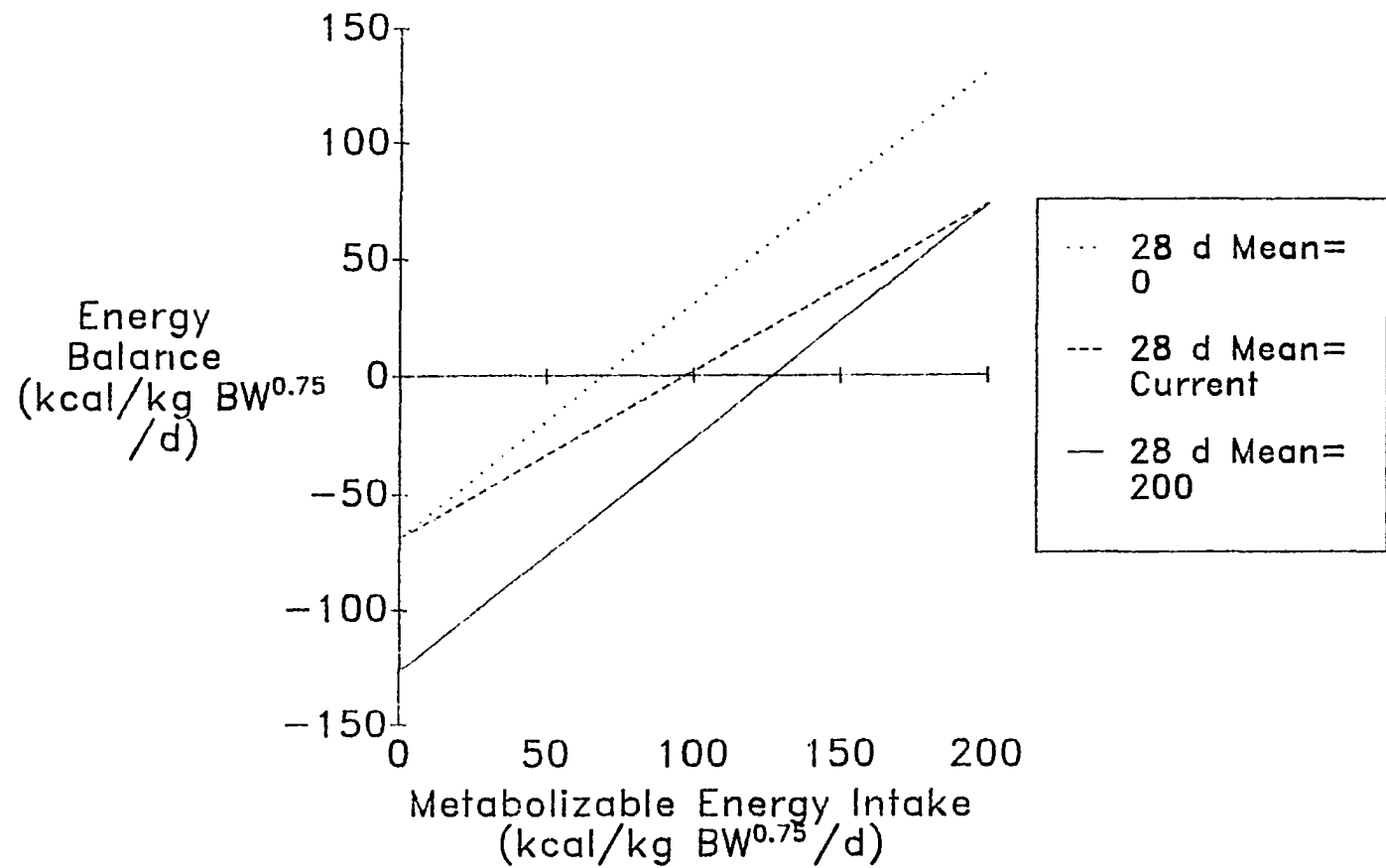


Fig. 24. Conceptual diagram of the effect of previous feeding level on energy requirements.

animal that had received 200 kcal/kg $BW^{0.75}/d$ for the previous 28 d and the dotted line indicates where the animal was starved (0 kcal/kg $BW^{0.75}/d$) for the previous 28 d.

Clearly, the solid line indicates that the efficiency of retaining energy is low, since the animal's requirements for RM were higher. The dotted line depicts the potential increased energy retention efficiency and lower maintenance requirements of an animal which had been starved for 28 d prior to offering increasing levels of feed. The dashed line (Fig. 24) shows the efficiency is high, because less of the consumed energy was required to meet RM demands. Not only are the maintenance estimates different among the treatments but also the efficiency (slope of the line) is different. However, this response is only temporary and the dotted (0 plane) and the solid (200 plane) lines will decrease to equal the solid line in a 28 d adaptation period.

To isolate plane-of-nutrition effects, the model simulation data were subjected to a separate regression analysis of energy balance on digestible energy intake (Fig. 25). Maintenance requirements were estimated from the model's yearly simulation. Digestible energy requirements for the animals below maintenance were lower than that for animals above maintenance (109.5 vs. 126.0, respectively) (Fig. 25). The mean RM of animals above maintenance (94.4

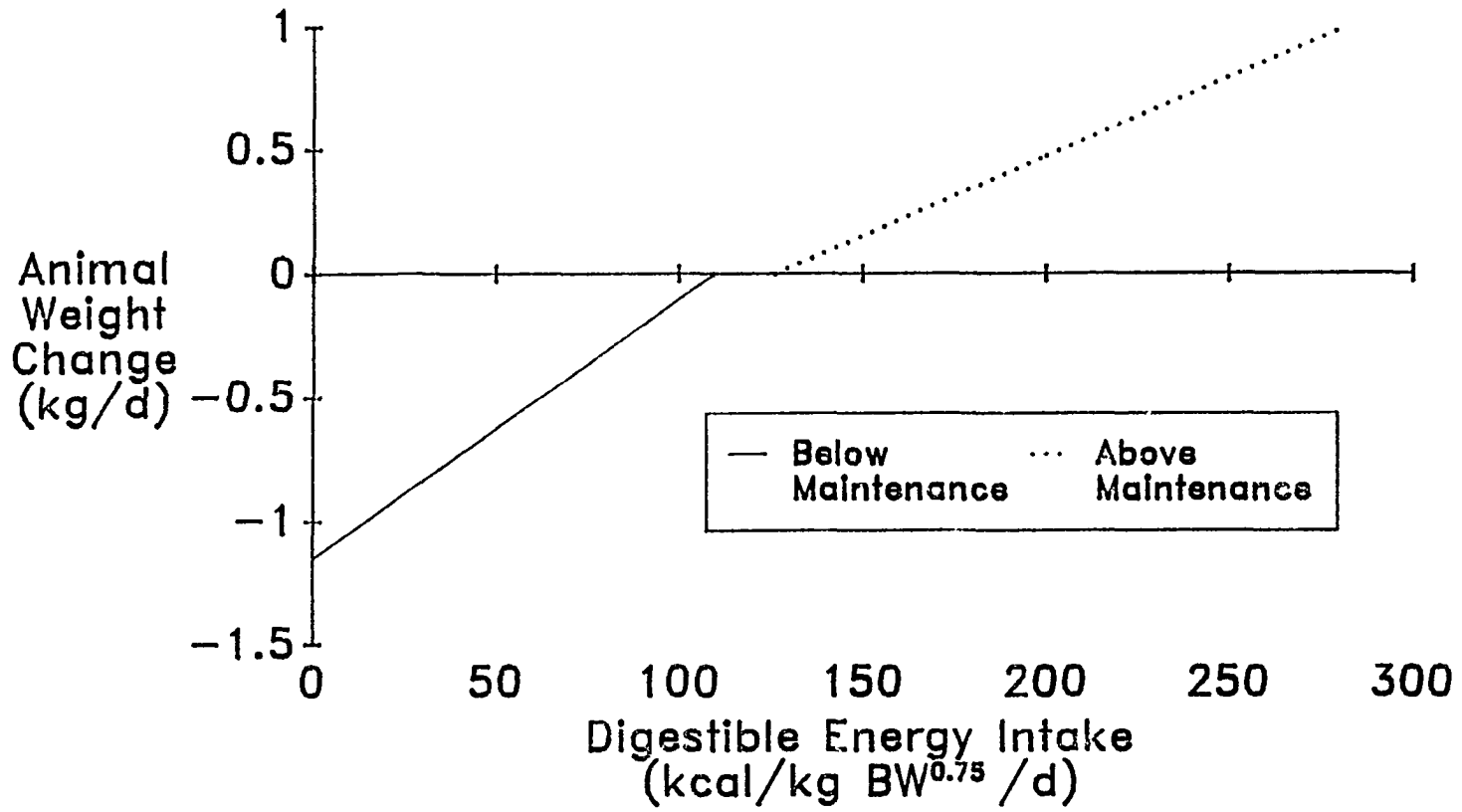


Fig. 25. Model-estimated energy balance above and below maintenance for an adult nonproductive female moose.

sd=5.34) was higher than for animals below maintenance (81.9 sd=8.28). This 12.5 kcal/kg $BW^{0.75}/d$ difference in energy available to the animal partially explains the difference in maintenance estimates for animals above and below maintenance (i.e., gap between the 2 lines at maintenance).

The difference in slopes (Fig. 25) is due to 2 factors: the manner in which weight loss and gain occurred (i.e., loss of 70% fat, 30% lean; gain of 70% lean, 30% fat until $EXLBW=LBW$ then 100% fat; Eq. 13 - 23) and the previous level of intake. The difference in slopes is dependent on how the energy available for production is utilized by the animal and the relative efficiency of the use (i.e., lactation, growth, and fattening) (Van Soest 1982).

Resting Metabolism

Because maintenance requirements are highly dependent on RM of the animal, a simulation of seasonal RM is shown in Fig. 26. In the fall (Julian days 221-334) RM is fairly constant but high (mean=93.2 sd=3.49). The summer period selected was Julian days 103-220; variation was high and the mean RM was 91.4 (sd=9.89). During the winter period (Julian days 335-102) the lowest RM (85.7, sd=10.6) was recorded. The high variation in RM during both the summer and winter periods was related to large shifts in energy intake during these periods.

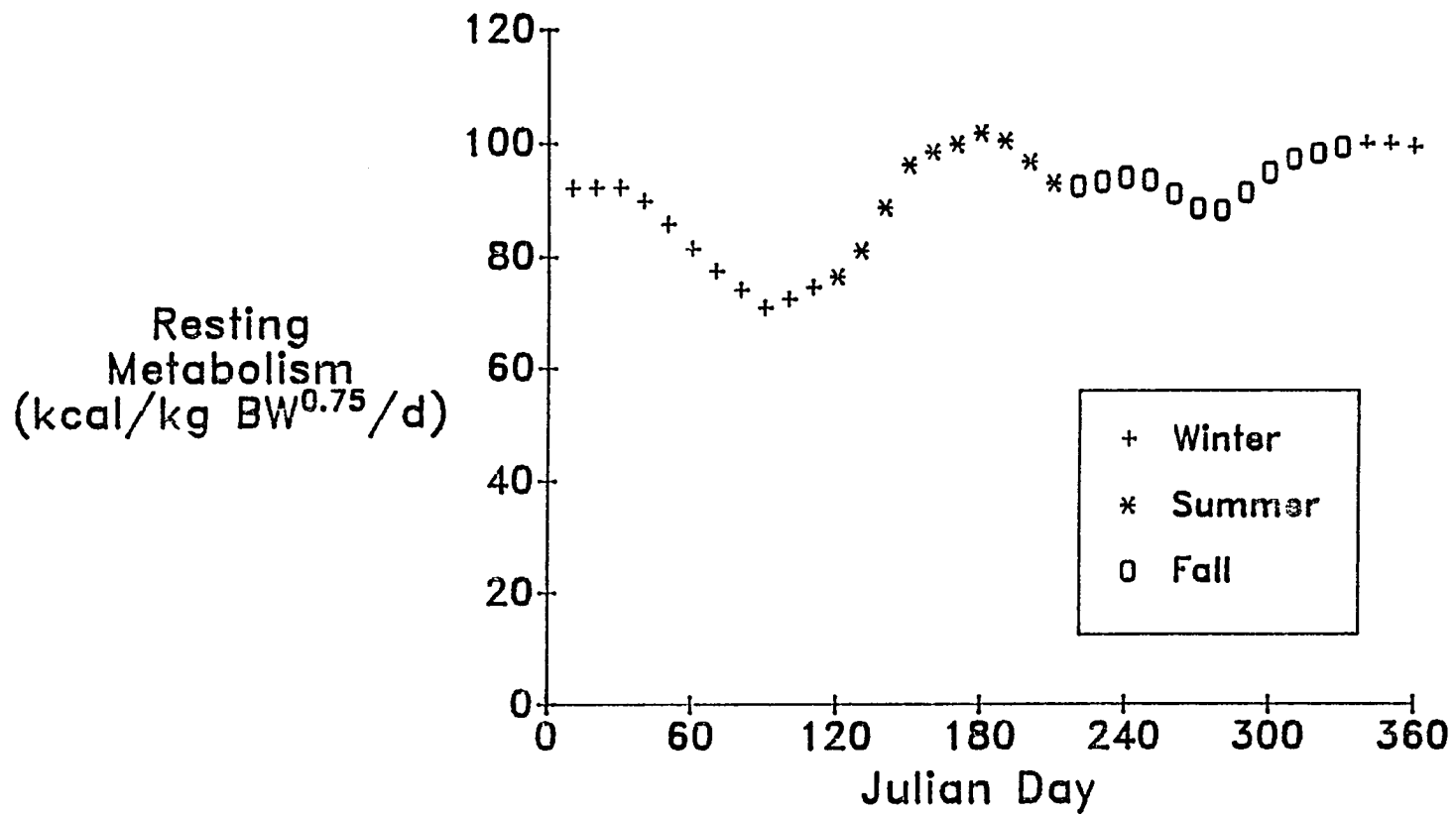


Fig. 26. Model-estimated seasonal resting metabolism of an adult nonproductive female moose.

CONCLUSIONS

This model was developed to evaluate the use of body condition to derive seasonal food intake and evaluate seasonal energy requirements. The model's strength is in its evaluation of energy requirements (Fig. 27), since it allows the flexibility of changing maintenance energy requirements.

The mechanism of food intake control cannot be determined from this model; however, using seasonal body condition targets to "guide" simulated intake is beneficial. It is doubtful that energy intake is independently controlled by body fat, but probably a host of factors (i.e., photoperiod, hormones) (Fig. 28).

One weakness of the model is the rigidity in which body condition controls intake. This may not be a function of the model alone but rather shows the importance of daily satiety control (i.e., gut fill).

The model allows intake to go to 0 or as high as MXINTAKE within 1 day. This is surely in error and could be alleviated by a daily subroutine which would restrict the animal to a minimal daily intake and gradual changes in daily intakes.

This model enhances understanding of seasonal energy partitioning and control of food intake. Further knowledge of these areas allows the biologist to come 1 step closer to

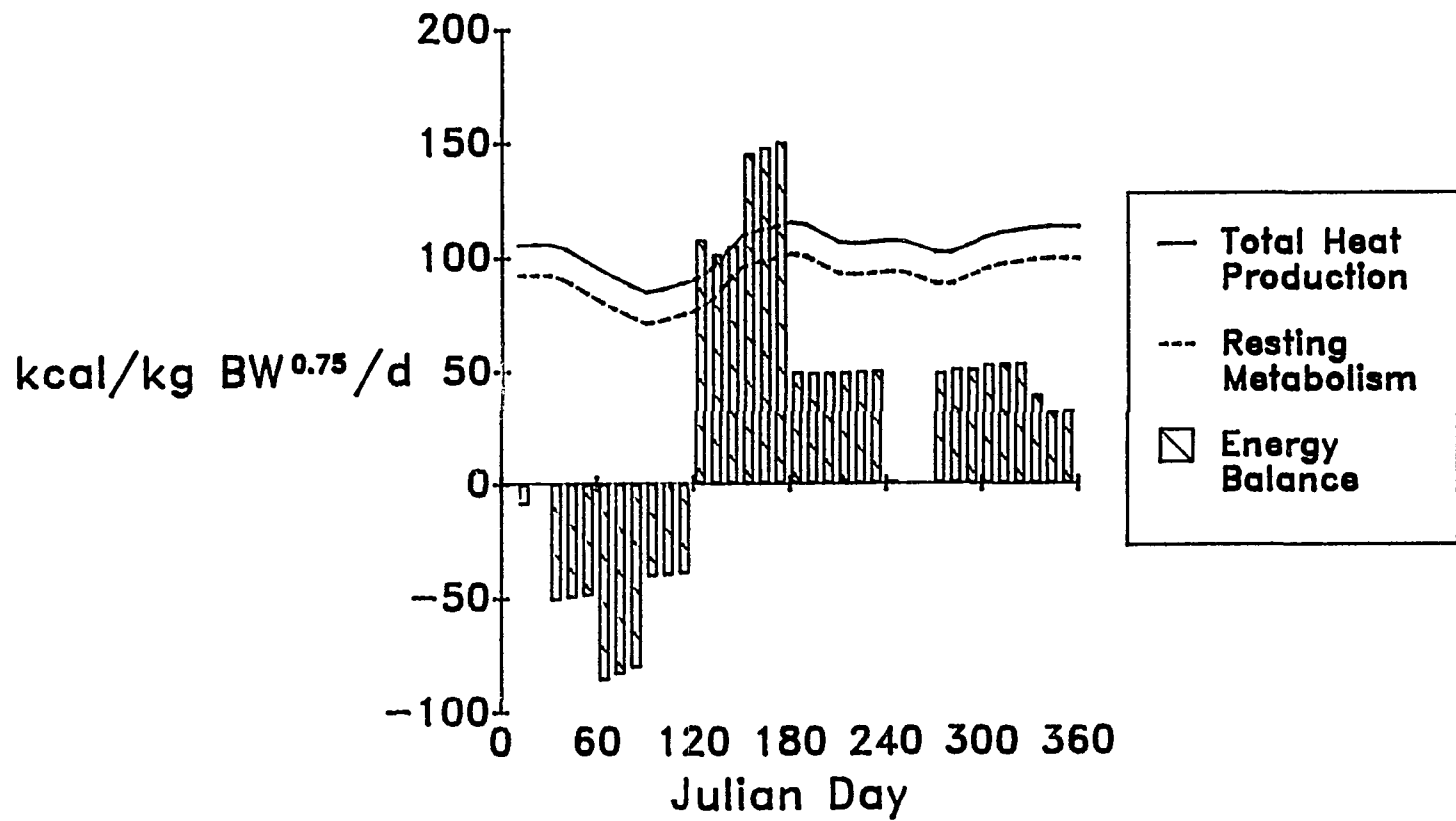


Fig. 27. Model-estimated relationships between total heat production, resting metabolism, and energy balance. These estimates are for an adult nonproductive female moose.

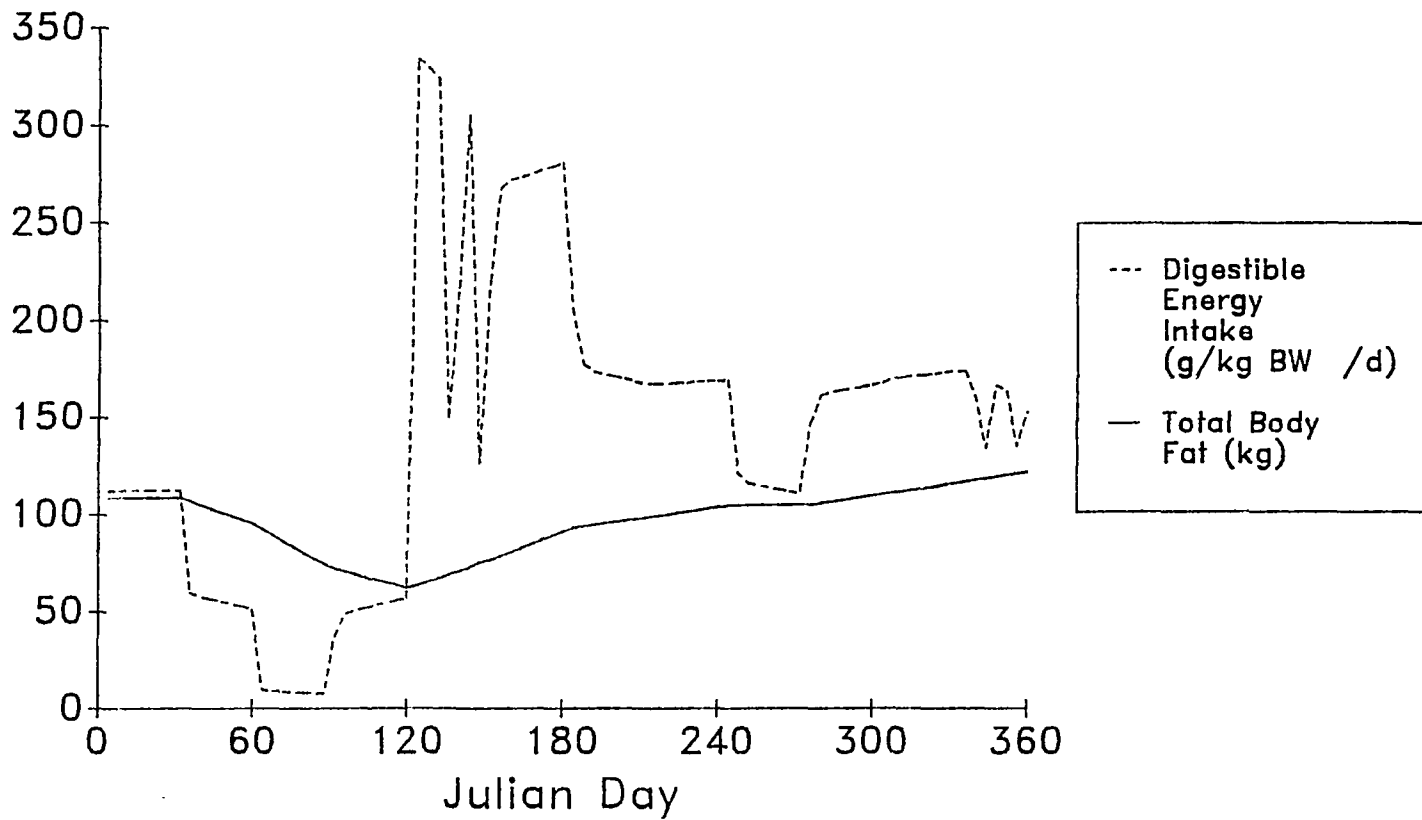


Fig. 28. Comparison of model-estimated digestible energy intake and predicted total body fat of an adult nonproductive female moose.

developing a carrying capacity model with which to manage moose.

SYNOPSIS AND CONCLUSIONS

The relationship between forage quality and energy partitioning is important to further the understanding of seasonal nutritional status of moose. Food intake, diet digestibility, and fasting metabolism have the greatest effects on animal production in simulated energy budgets of caribou. Therefore, insight into factors controlling food intake, diet digestibility, and metabolic rate are important in developing an understanding of the strategies evolved by moose to meet their seasonal energy requirements.

Chapter 1

In Alaska, winter browse supply and its nutritive quality are important to moose range carrying capacity. In many areas of southcentral Alaska, early stages of forest succession provide an abundance of excellent moose forage (i.e., aspen and willow). As the vegetation changes the habitat becomes dominated by paper birch. In areas of high moose density in southcentral Alaska, paper birch becomes the dominant item in the moose diet even though it is less preferred than willow or aspen.

Winter forage quality limits forage intake for moose. This study was conducted to determine if increasing browsing pressure reduces the quality of forage harvestable by moose.

Moose browsing point diameters (i.e., the diameter of the point where moose browse the twig) of paper birch was determined in each of 4 treatments. The nutritional quality of paper birch consumed in each of the treatments was estimated by using the mean browse point diameter from each treatment and predicting the nutrient content of the harvested twig. The nutritive quality of harvested twigs was estimated from nutritional analysis of twigs clipped at a range of diameters. Nutritional quality was inferred from measurement of in vitro dry matter disappearance (IVDMD), crude protein (CP), and fiber.

I hypothesized that increasing use of paper birch by moose would increase the browse point diameter, thus reducing forage quality of harvested paper birch. This hypothesis was rejected as browsing point diameter of paper birch was not different among the 4 treatments (23, 31, 41, and 66% utilization). Because browse point diameters were not different among treatments, estimated nutritional qualities were not different.

However, nutritional quality of paper birch did decrease with increasing diameter. Testing 4 different regression models (i.e, linear, multiplicative, logarithmic, and exponential models) showed that the multiplicative model best estimated the decrease in crude protein, neutral detergent solubles (cell contents), or IVDMD as twig diameter increased.

Chapter 2

Digestibility and intake of low-quality foods can be controlled by the retention time in the alimentary tract. Therefore, insight into the relationship between food intake and retention time in the digestive tract is important in understanding the winter feeding strategy of moose.

Furthermore, ruminal and alimentary capacity may vary seasonally. I hypothesized that a seasonal shift in alimentary fill and digesta flow through the alimentary tract exists in moose. In winter, when food quality and availability are low, alimentary fill is constant and passage rate increases with increasing food intake. Conversely, in spring/summer when forage quality and availability are high, alimentary fill is variable and retention time is positively correlated with intake.

Regression analysis of particle total mean retention time (h) on food intake ($\text{g}/\text{kg BW}^{0.75}/\text{d}$) indicated that as food intake decreased in winter, the particulate total mean retention times increased (slope = -1.22). In spring (Apr 1984-85), 2 trials indicated that an increase in food intake had a slight (slopes = -0.22 and -0.06) effect on particulate total mean retention times. The intercepts of linear regression (i.e., particle total mean retention time (Y) h on food intake (X) $\text{g}/\text{kg BW}^{0.75}/\text{d}$) were 114.4 for December and 62.4 and 54.4 h for the 2 April trials which indicate

that at 0 food intake digesta would be retained in the alimentary tract longer in the winter.

Alimentary fill in January did not increase as food intake increased, in fact it slightly declined. In the 2 spring trials, in contrast, alimentary fill increased slightly with increasing intakes. The intercepts of linear regression (i.e., alimentary fill (Y g/kg BW) on food intake ($X \text{ g/kg BW}^{0.75}/\text{d}$)) indicated that the alimentary fill at 0 intake is greater for the January trial (24.3) than the April trials (6.2 and 4.6 h).

These trials suggest that moose seasonally optimize forage nutrient intake by altering their digestive fill.

Chapter 3

Animals are required to expend a major portion of their food energy intake for physiological homeostasis (BMR). The measure of physiological homeostasis for ruminant animals is difficult, because heat production of the animal is influenced by feeding level.

Because prior feeding level influences BMR and large variations in seasonal intakes have been reported for moose, I hypothesized that much of the seasonal variation previously reported was due to prior feeding level. The objective of this study was to determine the effect of energy intake on the resting metabolism (lying, fed state) of moose and to

estimate the theoretical BMR (TBM). TBM was estimated as the Y intercept of the linear regression of animal heat production on metabolizable energy intake (MEI). Seasonal differences in TBM during December, February, and April were evaluated.

The results show that MEI kcal/kg BW^{0.75}/d had a significant effect on resting metabolism (RM) kcal/kg BW^{0.75}/d. Correlations between RM and MEI were done for different time periods (i.e., 7, 14, 21, 28, and 35) prior to measurement of RM, and the highest correlation of RM with MEI was found for the previous 28 d mean intake. The estimate of TBM was 68.8, 55.4, and 83.3 kcal/kg BW^{0.75}/d for trials 1 (Dec), 2 (Feb), and 3 (Apr), respectively. However, estimated TBM was not significantly ($p < 0.05$) different among the trials.

The pooled (i.e., trials 1, 2, and 3) linear regression model (i.e., $RM = 68.6 + 0.289 * MEI$) is useful in animal simulation models. Currently, the most common procedure for estimation of animal heat production is estimation of BMR, estimation of heat increment, and summing the 2 values. The relation between RM and MEI provides an estimate of heat production without the uncertainty of additive models.

During the 3 trials, feed intake was significantly different among the 3 diet quality treatments (1.99, 2.26, and 2.61 metabolizable energy kcal/g). However, the caloric

intake was not different among treatments, suggesting that animals ate to caloric fill rather than alimentary fill.

Chapter 4

The simulation model presented in Chapter 4 proved useful in molding together ideas, speculations, and the results of Chapters 2 and 3. This simulation model predicts intake and energy requirements of moose based on an assumption that moose have innate seasonal body condition targets. These target body condition levels were derived by feeding moose a pelleted diet ad libitum throughout the year and estimating seasonal body condition.

In the model, food intake is controlled by both a maximum alimentary fill and by caloric fill (i.e., energy required to achieve target body condition). The model allows the moose to eat until its caloric requirements have been met or the maximum alimentary fill is achieved.

Resting metabolism is not constant in the model, but rather a response to energy intake. This allows for seasonal changes in resting metabolism as ingested energy intake changes to meet energy demands for production of body tissue. Therefore, resting metabolism changes seasonally, and maintenance requirements change seasonally.

The model proved useful in predicting seasonal energy requirements. The model predicted winter (Nov 21-Apr 22)

maintenance requirement for the nonproductive female was 122.2 compared with experimental results of 140.8 (kcal/kg $BW^{0.75}/d$).

Predicted food intakes by the model were very erratic with large daily fluctuations. This is in response to body condition targets that were changed on a monthly basis. Furthermore, food intake in the model was restricted only by a calculated upper limit (i.e., maximum intake) and a lower limit of 0 intake. Therefore, daily intakes could make excursions from maximum intake to 0 intake on consecutive days. The model should be modified to allow for satiety control of food intake, thereby establishing a minimum intake level above 0 which would reduce daily intake fluctuations.

This model's strong point is its flexibility in allowing the "animal" to alter body condition. In most ruminant simulation models, intake is regulated by alimentary fill alone, thereby setting intake. This model allows an animal to gain or lose weight depending on the forage quality and body condition targets independent of the season of year.

Important Findings

Chapter 1:

- 1) Increasing utilization of paper birch (UT; \pm 80% C.I.) by moose from 23 to 66% of potential availability did not

significantly increase moose mean browse point diameter
(MBP; mm):

Pen 1 UT 41 ± 11; MPB=2.64; sd=1.18

Pen 2 UT 23 ± 10; MBP=2.55; sd=1.10

Pen 3 UT 31 ± 14; MBP=2.50; sd=0.95

Pen 4 UT 66 ± 10; MBP=2.83; sd=0.96

2) Regression analysis of nutrient content of paper birch on diameter (2, 3, 4, 5, 6, 7, 8, 9 mm) showed that a multiplicative model ($Y=aX^b$) provided the best fit for:

Crude Protein $Y=10.5 X^{-0.348}$; SE est 0.048;

$r=-0.971$; $n=7$

Neutral Detergent Solubles $Y=50.46 X^{-0.422}$

SE est 0.034; $r=-0.990$; $n=7$

In Vitro Dry Matter Disappearance $Y=31 X^{-0.384}$

SE est 0.070; $r=-0.919$; $n=6$

3) Because nutritional quality of paper birch varies with diameter, I recommend that forage collected for nutritional analysis should be clipped to the observed mean browse point diameter.

4) Since the browse point diameters were not different among different utilization levels, the predicted nutritive quality of paper birch was not different among treatments.

5) Digestive inhibitors appeared to alter the digestibility or predicted digestibility of the paper birch. Plant secondary compounds may have caused an overestimation of

neutral detergent solubles, thereby reducing digestibility below that predicted by the VanSoest formula. An alternative explanation was that the secondary chemicals inhibited digestion in vitro of the paper birch.

Chapter 2

6) These results indicate that moose optimize energy intake in winter by altering food retention time in the alimentary tract and maintaining a constant alimentary fill. This allows rapid movement of the poorly digestible material through the alimentary tract if intake is high. However, during periods of low intake (e.g, low availability) retention time in the digestive tract increases to enhance nutrient extraction.

In spring/summer the digestive strategy of moose appears to link alimentary fill with intake, thereby increasing alimentary fill as food intake increases. Furthermore, increasing food intake has only a slight influence on retention time of digesta in the alimentary tract. This strategy allows the moose to increase intake of spring/summer plant material, which has a rapid rate of digestion, while minimizing the expected decrease in digesta retention time. Increased retention time of spring/summer forage material would not likely enhance digestibility.

Chapter 3

7) Metabolizable energy intake (X) kcal/kg $BW^{0.75}/d$ had a significant effect on resting metabolism (Y) kcal/kg $BW^{0.75}/d$ in moose.

$$\text{Resting Metabolism } Y=68.8+0.289X \quad r=0.522;$$

$$\text{SE est } 10.17; \quad n=20$$

8) The theoretical BMR was not different ($p<0.05$) among December (68.8; SE=24.09; n=7), February (55.4; SE=15.01; n=7) or April (81.3; SE=29.95; n=6). However, since there is a large error associated with the TBM estimate, the results on seasonal trends are inconclusive.

9) Metabolizable energy intake had no effect on respiratory quotient (RQ), though the RQ was significantly lower in February (0.61; sd=0.50) than December (0.72; sd=0.74) or April (0.78;sd=0.13).

10) During the 3 trials, feed intake (g/kg $BW^{0.75}/d$) was significantly different among the 3 diet quality treatments (1.99, 2.26, and 2.61 metabolizable energy kcal/g). However, the caloric intake was not different among treatments, suggesting that animals ate to meet a minimal caloric requirement.

Chapter 4

11) The moose simulation model was based on the assumption that moose have seasonal body condition targets which they

attempt to achieve by altering food intake. This assumption could not be tested in the model, but the model output was in good agreement with reported estimates of seasonal energy requirements.

12) Sensitivity analysis of the moose simulation model showed that a 10% increase in digestibility reduced yearly intake by -10.9%. This is contrary to previously reported sensitivity analysis but is due to physiological control of intake rather than physical control of intake.

13) Sensitivity analysis (+10%) of the variables for resting metabolism, total mean retention time, maximum intake and daily activity costs increased yearly food intake by 7.6, 6.5, 6.5, and 0.9%, respectively.

Management Implications

Understanding the limits and abilities of the land to support animal populations is essential in providing additional information for wildlife biologists. Estimation of nutritional quality of the forage utilized by moose should not be done using the classical method based on current annual growth as the main criterion. This study shows that an estimate of the browse point diameter should be made to estimate both food availability on the range and the nutritional quality of the forage.

Estimates of seasonal food intakes and body condition provided by the simulation model allow the biologist to compare best case:worst case scenarios for managed animal populations. The full usefulness of this type of model will be realized when it is integrated into a population model that relates range to body condition to reproductive performance in order to predict population trends with time.

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APPENDIX A. The moose simulation model described in Chapter 4. This model is in IBM basic.

```
10 FOR KK=1 TO 10:PRINT:NEXT KK
20 PRINT
30 PRINT"                MRCMODEL                "
40 PRINT
50 PRINT"                FORAGE UTILIZATION MODEL FOR MOOSE"
60 PRINT" INTAKE REGULATED BY BODY CONDITION AND MAXIMUM ALIMENTARY FILL"
70 PRINT
80 PRINT"                M.E. Hubbert & C.C. Schwartz "
90 PRINT
100 PRINT"                SEPTEMBER 1966 "
110 PRINT
120 PRINT"                VERSION 3.9 "
130 PRINT
140 PRINT
150 PRINT
160 PRINT
170 PRINT
180 PRINT
190 PRINT
200 TBW2=450
210 FOR JJ=1 TO 5:PRINT:NEXT JJ
220 '        ***** DIMENSION STATEMENTS FOR INPUTS *****
230 DIM DIG(2,12), NITRO(2,12), FAT(2,12), STAND(2,12), WALK(2,12), M(12)
240 DIM M1(12), LYING(2,12), FEEDING(2,12), AVAIL(2,12), XO(2,14), MNH$(12)
250 DIM SUM(500),CT(500)
260 '        ***** INPUTS FOR NITROGEN CONTENT *****
270 FOR I%= 1 TO 2 : FOR J%= 1 TO 12 : READ NITRO(I%,J%) : NEXT J%: NEXT I%
280 DATA 32,60,91,121,152,182,213,244,274,305,335,366
290 DATA .0107,.01088,.0112,.03,.025,.025
300 DATA .025,.0214,.0214,.01014,.01053,.01056
310 '        ***** INPUTS FOR DIGESTIBILITY OF THE DIET *****
320 FOR I%= 1 TO 2 : FOR J%= 1 TO 12 : READ DIG(I%,J%) : NEXT J%: NEXT I%
330 DATA 32,60,91,121,152,182,213,244,274,305,335,366
340 DATA .312,.315,.333,.56,.531,.531
350 DATA .447,.420,.396,.376,.35,.315
360 '        ***** INPUTS FOR DESIRED % FAT AT MONTHLY INTERVALS *****
370 FOR I%= 1 TO 2 : FOR J%= 1 TO 12 : READ FAT(I%,J%) : NEXT J%: NEXT I%
380 DATA 32,60,91,121,152,182,213,244,274,305,335,366
390 DATA 24,22,18,16,18,21,22,23,23,24,25,26
400 '***** ACTIVITY DATA FROM RENECKER AND HUDSON *****
410 '***** BASED ON PERCENT OF DAY AT EACH ACTIVITY *****
420 '***** COSTS ARE BASED ON KCAL/HR/KGBW0.75 *****
430 '        ***** INPUTS FOR % OF THE DAY STANDING *****
```

```

440 FOR I%= 1 TO 2 : FOR J%= 1 TO 12 : READ STAND(I%,J%) : NEXT J%: NEXT I%
450 DATA 32,60,91,121,152,182,213,244,274,305,335,366
460 DATA 4.7,4.7,4.7,4.7,4.7,4.7,4.7,4.7,4.7,4.7,4.7,4.7
470 ' ***** INPUTS FOR % OF THE DAY WALKING *****
480 FOR I%= 1 TO 2 : FOR J%= 1 TO 12: READ WALK(I%,J%) : NEXT J%: NEXT I%
490 DATA 32,60,91,121,152,182,213,244,274,305,335,366
500 DATA 2.3,2.3,2.3,2.3,2.3,2.3,2.3,2.3,2.3,2.3,2.3,2.3
510 ' ***** INPUTS FOR % OF THE DAY LYING *****
520 FOR I%= 1 TO 2 : FOR J%= 1 TO 12 : READ LYING(I%,J%) : NEXT J% : NEXT I%
530 DATA 32,60,91,121,152,182,213,244,274,305,335,366
540 DATA 51.9,51.9,51.9,51.9,51.9,51.9,51.9,51.9,51.9,51.9,51.9,51.9
550 ' ***** INPUTS FOR % OF THE DAY FEEDING *****
560 FOR I%= 1 TO 2 : FOR J%= 1 TO 12 :READ FEEDING(I%,J%):NEXT J% : NEXT I%
570 DATA 32,60,91,121,152,182,213,244,274,305,335,366
580 DATA 40.6,40.6,40.6,40.6,40.6,40.6,40.6,40.6,40.6,40.6,40.6,40.6
590 ' *** INPUTS % OF INTAKE THAT CAN BE OBTAINED *****
600 FOR I%= 1 TO 2 : FOR J%= 1 TO 12 : READ AVAIL(I%,J%) : NEXT J% : NEXT I%
610 DATA 32,60,91,121,152,182,213,244,274,305,335,366
620 DATA 100,100,100,100,100,100,100,100,100,100,100,100
630 ' ***** DETERMINES THE NUMBER OF DAYS IN A MONTH *****
640 FOR I%= 1 TO 12 :READ M(I%): NEXT I%
650 DATA 32,60,91,121,152,182,213,244,274,305,335,366
660 LET MNTH$="JANFEBMARAPRPMAYJUNJULAUAGSEPOCTNOVDEC"
670 FOR I%=1 TO 12 : J%=(I%-1)*3 + 1 : MNH$(I%) = MID$(MNTH$,J%,3) : NEXT I%
680 '***** OPENING AN OUTPUT FILE *****
690 INPUT " DO YOU WANT OUTPUT TO A FILE Y OR N ";ANS$
700 IF ANS$="Y" THEN 710 ELSE 760
710 INPUT " ENTER OUTPUT FILE NAME";FIL$
720 INPUT " ENTER NUMBER OF DAYS BETWEEN OUTPUT TO FILE (DBY)";DBY
730 OPEN FIL$ AS #1 LEN=58
740 FIELD #1,5 AS Z$,8 AS B$,8 AS C$,6 AS D$,8 AS E$,8 AS F$,13 AS GGG$
750 FIELD #1,45 AS GG$,8 AS F1$,3 AS F3$, 1 AS G$, 1 AS H$
760 INPUT"NUMBER OF DAYS BETWEEN OUTPUT TO THE SCREEN";GOUTS
770 INPUT" ANIMAL AGE IN DAYS";AGEDAYS
780 INPUT" TOTAL BODY WEIGHT (KG)";TBW
790 INPUT" TOTAL BODY FAT (KB)";TBF
800 INPUT" MAXIMUM LEAN BODY WEIGHT TO BE ACHIEVED";M%LBW
810 INPUT" STARTING DAY FOR THE RUN (JULIAN DAY)";I1%
820 INPUT" ENTER ENDING DAY FOR THIS RUN";i2%
830 PRINT
840 PRINT" THESE NEXT INPUTS ARE USED IN VALIDATION"
850 PRINT" ENTER 1 FOR DEFAULT OR 1.1 FOR 10% INCREASE"
860 INPUT"DIGESTIBILITY FACTOR";XX2
870 INPUT"ACTIVITY FACTOR";XX1
880 INPUT"HEAT PROD. FACTOR";PPP
890 INPUT"TMRT FACTOR";PP1
900 INPUT"MAXINTAKE FACTOR";PF2
910 INPUT"FAT FACTOR";FP3

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920 INPUT " ARE ALL THESE INPUTS CORRECT (Y) OR NO (N) ";A#
930 IF A#="Y" THEN 950 ELSE 940
940 IF A#="y" THEN 950 ELSE 760
950 'LPRINT:LPRINT
960 ' LPRINT " ANIMAL AGE IN DAYS";AGEDAYS
970 'LPRINT " TOTAL BODY WEIGHT";TBW
980 'LPRINT " TOTAL BODY FAT (KG)";TBF
990 'LPRINT " MAXIMUM LEAN BODY WEIGHT TO BE OBTAINED";MXLBW
1000 'LPRINT " START AND ENDING DAY FOR THIS RUN ";I1% ;I2%
1010 'LPRINT " DIGESTIBILITY MULTIPLIER =";XX2
1020 FOR IJJ= 1 TO 4 : PRINT ;NEXT IJJ
1030 MXAGED=3000 : '*** MAXIMUM AGE IN DAYS
1040 KCALSG=4.45 : '*** KCALS / GRAM ENERGY IN FORAGE
1050 LBW=TBW-TBF : ' ***** CALCULATES LEAN BODY WEIGHT
1060 CT=2S : '*** THIS IS A COUNTER FOR RM INTAKE
1070 LET KB = I1% - 1 : ' **** KB IS THE VALUE FOR KEEPING TRACT OF DAY
1080 INTAKE=7000 : ' **** SETS STARTING VALUE FOR INTAKE
1090 BINTAKE=70 : '**** THIS IS JUST A STARTING VALUE
1100 MTBW=TBW
1110 FOR I% = I1% TO I2%
1120 LET B3=I%
1130 LET O7=B3
1140 LET KB=KB+1
1150 IF KB>365 THEN LET KB=KB-365
1160 FOR JX=1 TO 12
1170 LET M8%=MNH$(JX)
1180 IF JX=1 THEN GOTO 1220
1190 LET D=KB-M(JX-1)+1
1200 GOTO 1240
1210 NEXT JX
1220 LET D=KB
1230 IF O7>365 THEN O7=O7 - 365
1240 ' ***** CALCULATION FOR DIGESTIBILITY OF THE DIET *****
1250 FOR IQ%=1 TO 2:FOR JQ%=1 TO 12:X0(IQ%,JQ%)=DIG(IQ%,JQ%)
1260 NEXT JQ%;NEXT IQ%
1270 LET X=KB
1280 LET N=12
1290 GOSUB 3470
1300 XDIG=Z1*XX2
1310 ' ***** CALCULATION FOR NITROGEN IN THE DIET *****
1320 FOR IQ%=1 TO 2:FOR JQ%=1 TO 12:X0(IQ%,JQ%)=NITRO(IQ%,JQ%)
1330 NEXT JQ%;NEXT IQ%
1340 LET X=KB
1350 LET N=12
1360 GOSUB 3470
1370 XNITRO=Z1
1380 ' ***** CALCULATION FOR COST OF TIME SPENT STANDING *****
1390 FOR IQ%=1 TO 2:FOR JQ%=1 TO 12:X0(IQ%,JQ%)=STAND(IQ%,JQ%)

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1400 NEXT JQ%:NEXT IQ%
1410 LET X=KB
1420 LET N=12
1430 GOSUB 3470
1440 XSTAND=Z1
1450 MSTAND=((XSTAND/100)*24)*60
1460 KSTAND=MSTAND*((.8122/60)*TBW^.75)
1470 ' ***** CALCULATION FOR THE COST OF TIME SPENT WALKING *****
1480 FOR IQ%=1 TO 2:FOR JQ%=1 TO 12:XO(IQ%,JQ%)=WALK(IQ%,JQ%)
1490 NEXT JQ%:NEXT IQ%
1500 LET X=KB
1510 LET N=12
1520 GOSUB 3470
1530 XWALK=Z1
1540 MWALK=((XWALK/100)*24)*60
1550 KWALK=MWALK*((1.8872/60)*TBW^.75)
1560 ' ***** CALCULATION FOR THE COST OF THE TIME SPENT LYING *****
1570 FOR IQ%=1 TO 2:FOR JQ%=1 TO 12:XO(IQ%,JQ%)=LYING(IQ%,JQ%)
1580 NEXT JQ%:NEXT IQ%
1590 LET X=KB
1600 LET N=12
1610 GOSUB 3470
1620 XLYING=Z1
1630 MLYING=((XLYING/100)*24)*60
1640 KLYING=MLYING*((.1433/60)*TBW^.75)
1650 ' ***** CALCULATION FOR THE COST OF THE TIME SPENT FEEDING *****
1660 FOR IQ%=1 TO 2:FOR JQ%=1 TO 12:XO(IQ%,JQ%)=FEEDING(IQ%,JQ%)
1670 NEXT JQ%:NEXT IQ%
1680 LET X=KB
1690 LET N=12
1700 GOSUB 3470
1710 XFEEDING=Z1
1720 MFEEDING=((XFEEDING/100)*24)*60
1730 KFEEDING=MFEEDING*((1.0332/60)*TBW^.75)
1740 ' ***** CALCULATIONS FOR % AVAILABLE *****
1750 FOR IQ%=1 TO 2:FOR JQ%=1 TO 12:XO(IQ%,JQ%)=AVAIL(IQ%,JQ%)
1760 NEXT JQ%:NEXT IQ%
1770 LET X=KB
1780 LET N=12
1790 GOSUB 3470
1800 XAVAIL=Z1
1810 ' ***** CALCULATION FOR DESIRED BODY FAT *****
1820 FOR IQ%=1 TO 2:FOR JQ%=1 TO 12:XO(IQ%,JQ%)=FAT(IQ%,JQ%)
1830 NEXT JQ%:NEXT IQ%
1840 LET X=KB
1850 LET N=12
1860 GOSUB 3470
1870 PFAT=Z1*PF3

```

```

1880 EXTBF=TBW*(PFAT/100)  : ' ** KG OF FAT DESIRED **
1890 DIFFTBF=(TBF-EXTBF)
1900 '          ***** PREDICTION OF LEAN BODY WEIGHT *****
1910 'AGEIDAY= AGE IN DAYS
1920 'EXLBW= EXPECTED LEAN BODY WEIGHT
1930 'MXLBW= MAXIMUM LEAN BODY WEIGHT TO BE OBTAINED
1940 'MXAGED= MAXIMUM DAYS IN AGE TO BE OBTAINED
1950 ' -9.1 = A VALUE USED THAT BEST EXPRESSES THE LINE FOR MOOSE
1960 EXLBW = MXLBW * (1 - EXP(-9.100001 * AGEIDAY)/MXAGED)
1970 'DIFFLBW=(LBW-EXLBW)
1980 IF EXTBF<TBF THEN 1990 ELSE 2060
1990 '***** WANT TO LOSS FAT WEIGHT *****
2000 BCEPF=DIFFTBF*9.399999*1000
2010 DIFFLBW2=DIFFTBF*.43:'**** LOSS OF LEAN BODY WEIGHT ***
2020 BCEPL=((.3056*(DIFFLBW2*1000))+(.6944*.449*(DIFFLBW2*1000)))/.29
2030 A$="LFL"
2040 TBF2=TBF-DIFFTBF:LBW2=LBW-DIFFLBW2
2050 GOTO 2180
2060 '***** WANT TO GAIN FAT WEIGHT *****
2070 IF EXLBW>LBW THEN 2080 ELSE 2130
2080 BCEPL=((DIFFTBF/.6)*2.3333)*5.3*1000) : '*****.5 IS EFFICIENCY
2090 BCEPF=(DIFFTBF*9.399999*1000)
2100 A$="GFL"
2110 TBF2=TBF-(DIFFTBF*.6):LBW2=LBW-((BCEPL/(2.3333*5.3*1000*.449)))
2120 GOTO 2180
2130 IF TBF>EXTBF THEN 2180 ELSE 2140
2140 BCEPF=((DIFFTBF/.6)*9.399999*1000)
2150 BCEPL=0
2160 A$="BF"
2170 LBW2=LBW:TBF2=TBF-(DIFFTBF*.6)
2180 '          ***** PREDICTION OF INTAKE *****
2190 IF INTAKE<10 THEN INTAKE=10 ELSE 2200
2200 BCEP=BCEPF+BCEPL
2210 '*** ADJUSTS MODEL FOR HIGHEST WEIGHT OBTAINED
2220 IF MXTBW<TBW THEN MXTBW=TBW ELSE 2230
2230 '*** THIS LINE ADDS UP ALL COSTS, SO WE KNOW HOW MUCH ENERGY WE NEED
2240 '***** TEST FOR MAXIMUM RUMEN FILL *****
2250 TMRT=(60.86-(.2366*(INTAKE/TBW^.75)))*PP1
2260 MXVN=(140*MXTBW^.75)*((1-.56)*(TMRT/24))
2270 VN=INTAKE*(1-XDIG)*(TMRT/24)
2280 MXINTAKE=(MXVN+(MXVN*XDIG)/(2*(1-XDIG)))*PP2
2290 '***** THIS ADJUSTS HOW MUCH THEY CAN EAT BY REDUCING RUMEN FILL
2300 IF MXINTAKE>INTAKE THEN 2350 ELSE 2310
2310 INTAKE=MXINTAKE:MAX=1:'THIS IS TO TELL THAT MAX INTAKE
2320 GOTO 2560
2330 'IF TBF>EXTBF THEN 2050 ELSE 2320
2340 '***** TESTS INTAKE AGAINST EBALANCE *****
2350 INTKCAL=INTAKE*KCALSG

```

```

2360 RM=((68.8+.289*5INTAKE)*TBW^.75)*PPP
2370 ACTKCAL=(KSTAND+KWALK+KFEEDING+KLYING)*XX1
2380 IBW = INTAKE/TBW^.75
2390 GUN=(.5607*((XNITRO*INTAKE)*TBW^.75)+.05607)/TBW^.75 ;'** G NITR
2400 URINEE=307.3 + (8.327*GUN): '** KCALS FROM URINE NITRO
2410 FECALE=INTAKE*(1-XDIG)*KCALSG
2420 DINTAKE=INTKCAL-FECALE
2430 MEINTAKE=(INTKCAL-(FECALE+URINEE))/TBW^.75
2440 METHANEE= -1*(3.64 + (7.5 * DIG) + (DINTAKE/130 *(1.03 - (2.8 * DIG))))
2450 NETE=INTKCAL-(FECALE+METHANEE+URINEE+RM+ACTKCAL):'NET ENERGY
2460 '***** EBALANCE --INTAKE- ALL COSTS AND ENERGY POOL *****
2470 ANIMALEB=INTKCAL-(FECALE+URINEE+RM+METHANEE+ACTKCAL)
2480 EBALANCE =BCEP+ANIMALEB
2490 ' ***** THIS CHANGES INTAKE TO ENERGY NEEDS *****
2500 IF INTAKE<0 THEN 2700 ELSE 2510
2510 IF EBALANCE<0 THEN 2520 ELSE 2540
2520 IF EBALANCE > -20 THEN 2560 ELSE 2530
2530 INTAKE=INTAKE+10: GOTO 2240
2540 IF EBALANCE < 20 THEN 2560 ELSE 2550
2550 INTAKE=INTAKE-10: GOTO 2240
2560 AGEDAYS=AGEDAYS +1 : '***** COUNTS THE DAYS
2570 SINTAKE=SINTAKE+(INTAKE/1000): '**** SUMS FOR INTAKE OVER TIME
2580 '***** TAKES THE LAST 28 DAY INTAKE MEAN FOR HEAT PRODUCTION
2590 MEI=INTAKE/TBW^.75
2600 CT=CT+1
2610 SUM(CT)=MEI
2620 FOR FF=CT-28 TO CT
2630 IF SUM(FF)<1 THEN 2660 ELSE 2640
2640 CT2=CT2+1
2650 CTINTAKE=CTINTAKE+SUM(FF)
2660 NEXT FF
2670 BINTAKE=CTINTAKE/CT2
2680 CTINTAKE=0
2690 CT2=0
2700 '***** THIS ADJUSTS BODY WEIGHT FOR SURPLUS OR ENERGY DEFICIT *****
2710 KCALS= ANIMALEB
2720 IF MAX=1 THEN 2730 ELSE 2840
2730 IF A$="GF" THEN 2750 ELSE 2740
2740 IF A$="GFL" THEN 2780 ELSE 2810
2750 IF ANIMALEB < 0 THEN 2780 ELSE 2760
2760 TBF= TBF+(ANIMALEB/(9.399999*1000))
2770 GOTO 2850
2780 TBF= TBF+((ANIMALEB*.7)/(9.399999*1000))
2790 LBW= LBW+((ANIMALEB*.3)/(5.3*1000))
2800 GOTO 2850
2810 TBF= TBF-ABS((ANIMALEB*.7)/(9.399999*1000))
2820 LBW= LBW-ABS((ANIMALEB*.3)/(5.3*1000))
2830 GOTO 2850

```

```

2840 TBF=TBFE; LBW=LBWE
2850 TBW=TBF+LBW
2860 W7=W7+1
2870 WW7=WW7+1
2880 XFAT=(TBF/TBW)*100
2890 IF XFAT< 5 THEN 2900 ELSE 2920
2900 IF XFAT<3 THEN 2910 ELSE PRINT"ANIMAL IS....NONPRODUCTIVE" :GOTO 2920
2910 PRINT" THIS ANIMAL PROBABLY IS DEAD... BODY FAT BELOW 3% ": 'GOTO 3220
2920 XSUMINT=XSUMINT + INTAKE
2930 XSUMINT2=XSUMINT2+INTAKE
2940 IF MTBW<TBW THEN MTBW=TBW ELSE 2950
2950 MEINT=INTAKE/TBW^.75
2960 MEINT1=MEINT1+MEINT
2970 IF W7<OUTS THEN 3250
2980 W7=0
2990 FOR IK=1 TO 6 : PRINT : NEXT IK
3000 'LPRINT:LPRINT:LPRINT
3010 'LPRINT "          JULIAN DAY  ";KB
3020 '***** PRINT STATEMENTS *****
3030 PRINT "TOTAL BODY WEIGHT (TBW)";TBW
3040 PRINT "LEAN BODY WEIGHT (KG)";LBW
3050 PRINT "EXPECTED LEAN BODY WEIGHT (EXLBW)";EXLBW
3060 PRINT "FAT WEIGHT (KG)";TBF
3070 PRINT "EXPECTED BODY FAT WEIGHT(EXTBF)";EXTBF
3080 PRINT "PERCENT BODY FAT ";(TBF/TBW)*100
3090 PRINT "INTAKE (KG)";INTAKE/1000:IF MAX=1 THEN PRINT"MAX INTAKE"ELSE 3100
3100 PRINT "INTAKE /KG BW.75 ";MEINT
3110 PRINT "TOTAL MEAN RETENTION TIME";TMRT
3120 PRINT "DIGESTIBILITY % ";XDIG*100
3130 PRINT "% FAT DESIRED";PFAT
3140 PRINT "SUM OF INTAKE";SINTAKE
3150 PRINT "MEAN INTAKE FOR LAST";OUTS"DAYS";XSUMINT/OUTS
3160 XXINT=(XSUMINT/OUTS)/TBW^.75
3170 XSUMINT=0
3180 XXMEI=MEINTAKE
3190 '***** ACTIVITY COSTS AND BENIFITS *****
3200 ACT1=(MEINTAKE*TBW^.75)/(KWALK+KSTAND+KFEEDING)
3210 ACT2=INTAKE/(MWALK+MSTAND+MFEEDING)
3220 'LPRINT"ME INTAKE / KCALS USED IN ACTIVITY";ACT1
3230 'LPRINT"INTAKE G / MINUTE SPENT ACTIVE";ACT2
3240 'LPRINT:PRINT
3250 IF WW7<DDY THEN 3440 ELSE 3260
3260 WW7=0
3270 IF DDY=0 THEN 3440 ELSE 3280
3280 XSUMI=XSUMINT2/DDY
3290 XXXINT=XSUMI/TBW^.75
3300 XSUMINT2=0
3310 IF ANS$="Y" THEN 3320 ELSE 3440

```

```
3320 CODE%=CODE%+1
3330 LSET Z$=STR$(KB)
3340 INTAKEN=INTAKE/TBW^.75:LSET B$=STR$(TBW)
3350 XHEAT=RM/TBW^.75:LSET C$=STR$(TBF)
3360 DINTAKEN=DINTAKE/TBW^.75:LSET D$=STR$(XXXINT)
3370 LSET E$=STR$(DINTAKEN)
3380 BINTAKEN=BINTAKE/TBW^.75:LSET F$=STR$(SINTAKE)
3390 MEINT2=MEINT1/DDY:MEINT1=0:LSET F1$=STR$(BINTAKE)
3400 LSET F3$=STR$(XHEAT)
3410 LSET G$=CHR$(13)
3420 LSET H$=CHR$(10)
3430 PUT #1,CODE%
3440 MAX=0 : '***** THIS RESETS MAX INTAKE TO 0
3450 NEXT I%
3460 PRINT:PRINT:PRINT" OUTPUT FILE NAME ";FIL$ :PRINT:STOP
3470 LET Z1=X0(2,1)
3480 IF X<X0(1,1) THEN GOTO 3570
3490 LET M% = N - 1
3500 FOR J% = 1 TO M%
3510 IF X>X0(1,J%+1) THEN GOTO 3550
3520 IF X0(1,J%+1)=X0(1,J%) THEN GOTO 3550
3530 LET Z1=X0(2,J%)+(X0(2,J%+1)-X0(2,J%))/(X0(1,J%+1)-X0(1,J%))*(X-X0(1,J%))
3540 GOTO 3570
3550 NEXT J%
3560 LET Z1=X0(2,N)
3570 RETURN
```